THE IMPACT OF MUSSEL (*Mytilus* SP.) FARMING ON ZOOPLANKTON COMMUNITIES IN NOTRE DAME BAY NEWFOUNDLAND

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The impact of mussel (*Mytilus* sp.) farming on zooplankton communities in Notre Dame Bay Newfoundland

By

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A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Masters of Science

Biology

August 2003

St. John's Newfoundland Canada

Abstract

This thesis examines the impact of mussel (*Mytilus* sp.) farming on cold water zooplankton communities as one component of a larger, interdisciplinary study of the environmental sustainability of shellfish aquaculture in Newfoundland. The mesozooplankton communities of two *Mytilus sp.* farms on the northeast coast of Newfoundland are compared to their hydrodynamically comparable reference sites, sampled quarterly in 2001-2002. Like many other shallow coastal areas, the zooplankton communities in Notre Dame Bay area are characterized by the predominance of several small species, including *Acartia* sp., *Pseudocalanus* sp., *Temora* sp. and *Oithona* sp. While the size distributions and total abundance were not significantly affected by mussel farming, the community composition of the farms differed from their reference sites in some study periods. The abundances of *Pseudocalanus* sp., *Acartia* sp., *Centropages* sp. and harpacticoid copepods were higher at the farms than at the reference sites while the abundances of copepod nauplii, *Oithona* sp. and *Temora* sp. were lower at the farms compared to the reference sites. These differences may be related to direct ingestion of some groups, differences between the food fields of farms and references, or competition with mussels for available food.

Acknowledgements

I would like to thank my supervisor, Don Deibel and my family and friends for their support and encouragment.

I would like to thank the field team on the AquaNet project EI 5 for the comraderie and assistance with sample collection. Thanks for all the help in the unpredictable Newfoundland weather. Gary Maillet at DFO, St. John's, provided assistance with the Multisizer.

Without the co-operation and assistance of Terry Mills (Black Gold, Inc.) and Joe Wiseman (Atlantic Ocean Farms) and their staff none of this work would have been possible.

This research was supported in part by funds from AquaNet, the Network of Centres of Excellence for Aquaculture.

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1.1 Rationale for study

Newfoundland's shellfish aquaculture industry has been expanding since the 1990s, reaching an export value of $3.8 million in 1999 (Newfoundland Aquaculture Industry Association). Blue mussels (*Mytilus edulis* and *M. trossulus*) are the primary species in cultivation. Mussel farms are found in highest density in Notre Dame Bay and along the south coast of Newfoundland. The increasing density of mussel farms has prompted the public, legislators and managers of coastal marine resources to question the degree to which shellfish farms might be influencing these ecosystems. However, studies of the potential impacts of bivalve farms are relatively few compared to those of fin-fish aquaculture. Furthermore, studies have been focused on the benthic impacts of oyster and mussel aquaculture in Europe where water quality was already compromised. The work reported in this thesis is part of a multidisciplinary study of the impacts of shellfish culture in Newfoundland. As such it represents the first impact study of mussel culture in Newfoundland and one of the first of cold water shellfish culture.

Bivalve aquaculture has three stages, namely spat collection, grow-out and harvesting. Spat can be collected through the use of collector ropes or by dredging. Nursery and grow out practices range from bottom culture to intertidal trestle culture or subtidal suspended culture (Kaiser et al, 1998). In Newfoundland the latter method is employed. The effects

of the grow-out phase of cultivation have received the most attention, specifically with respect to the benthos. The few existing studies of pelagic effects have been limited to examination of the depletion of chlorophyll *a* and to changes in sediment-water nutrient fluxes. Dilution and transport effects make it difficult to detect impacts in the pelagic system. Given their important role in coastal ecosystems, it is essential to determine the impact on zooplankton communities as part of the pelagic system.

1.2 Benthic impacts of shellfish culture

Different types of cultivation may impact the sediment through different means. For example, Spencer et al. (1997) suggested that the netting associated with bottom cultivation of clams contributed to a change in the infaunal community via disruption of hydrodynamics and an increase in sedimentation. However, mussel culture in Newfoundland is conducted using the long-line method (as it is in many locations around the world) wherein lines of mussels are suspended in the water column from buoys (Fig. 1.1). Mussel faeces and pseudofaeces drop from the ropes onto the seafloor below. It is through this biodeposition of faeces that benthic impacts may occur.

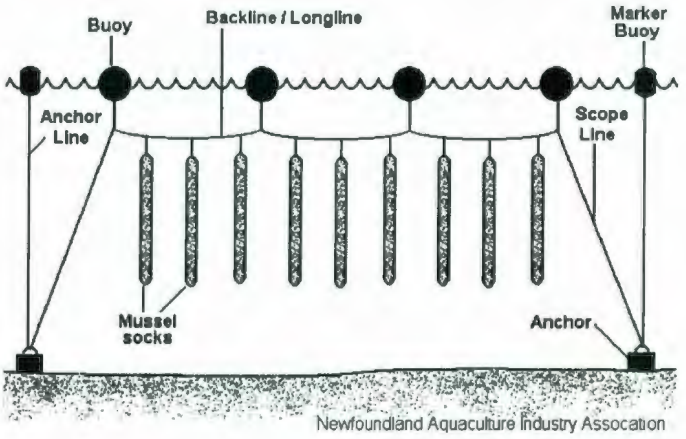

Figure 1.1: Longline culture setup as used by most Newfoundland mussel growers (Newfoundland Aquaculture Industry Association diagram)

Observed benthic impacts of shellfish aquaculture have included increased rates of sedimentation (Dahlback and Gunnarsson, 1981), organic enrichment resulting in high levels of sulfides and low levels of oxygen (Mirto et al, 2000; Stenton-Dozey et al. 2001), changes in sediment nitrogen cycling and fluxes (Barranguet, 1997; Gilbert et al, 1997; Kaspar et al, 1985), and in some cases, faunal disturbance with a decrease in diversity and an increase in the abundance of r-strategists (Mattson and Linden, 1983; Mirto et al, 2000). The presence and nature of impact has not been consistently negative, depending largely on the physical characteristics of the individual farms (Chamberlain et al, 2001; Kaiser et al, 1998). Although not in the identical biogeogrpahic region, work by Hatcher et al.(1994) and Grant et al (1995) in Nova Scotia, Canada is probably most applicable to Newfoundland farms. There, despite increased rates of sedimentation under mussel ropes at these farms, faunal diversity (as species number) did not change.

1.3 Pelagic impacts of mussel grazing

There are very few studies of the pelagic impacts of shellfish aquaculture. The studies that do exist have been restricted to determination of the amount of seston depleted by mussels, usually within the context of modeling the carrying capacity of farm sites for mussels. A review of these studies and studies of natural mussel beds and experimental manipulations in mesocosms suggests that the presence of a mussel farm has the potential to alter the pelagic ecosystem, including zooplankton.

Figure 1.2 illustrates some of the pathways of interactions between cultured mussels and benthic and pelagic systems. It is similar to that of naturally occurring mussel beds except that mussels in culture are often suspended in the water column, and mussels in culture are removed en masse for harvesting. In both systems, though, mussels consume suspended particles and either digest them or bind them into faeces and pseudofaeces resulting in their removal from the water column and as a food source for pelagic organisms such as zooplankton. In addition, mussels excrete ammonia into the water column which may stimulate primary production by nutrient-limited phytoplankton.

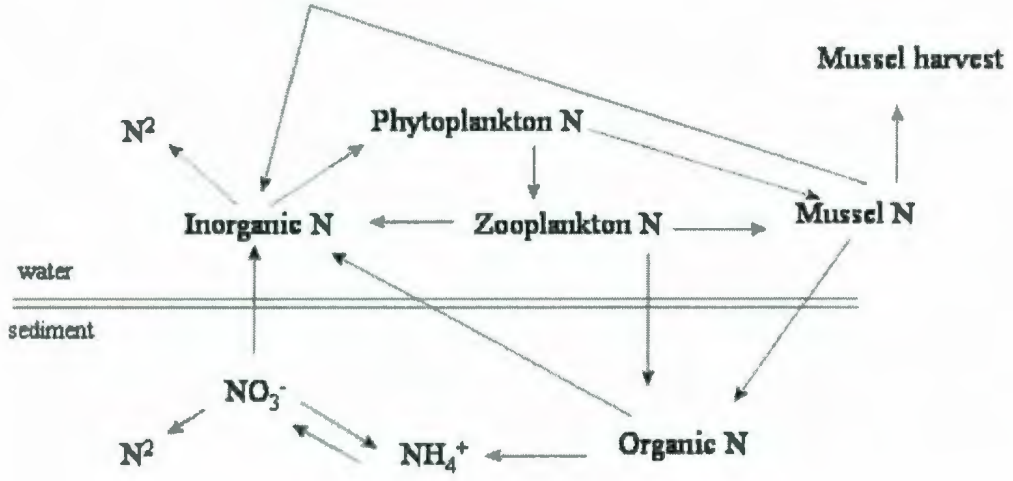

Figure 1.2: Nitrogen cycle of a mussel farm including zooplankton (adapted from Kaspar et al., 1985)

1.4 Ecosystems with wild mussels

Mussel beds are important natural recyclers of nutrients in a variety of coastal environments. The dynamics of their interactions with the ecosystem with respect to nutrient cycling, chlorophyll *a* levels in general and phytoplankton community composition in particular, may provide testable hypotheses regarding the impacts of mussels in culture on the surrounding ecosystem.

Natural populations of mussels have the ability to remove a very large proportion of the particulate matter from the water column, filtering the entire volume of fjords and other

partially enclosed water bodies in time frames ranging from hours (Horsted et al, 1988) to several days (Prins et al., 1994), sometimes leading to local seston depletion. On an inlet wide scale, the processing of large amounts of seston may speed the rate of nutrient recycling and reduce nutrient limitation of phytoplankton (Prins et al., 1998). Mussels capture small particles that would otherwise remain in suspension, removing them from the system. Their ammonia excretion may stimulate primary production..The stimulated primary production may sometimes balance the removal of particles by mussel feeding (Prins and Smaal, 1994). In the Baltic Sea, for example, mussel-driven nitrogen regeneration can account for 12 - 22% of the requirements for annual primary production (Kautsky and Evans, 1987).

The nature of the impact of bivalve grazing on plankton biomass varies but can extend over large geographic distances depending on the physical characteristics of an area. Plankton biomass was reduced by ~75% during passage over a natural *M. edulis* bed in a relatively open area in the Oresund and did not return to pre-bed levels for almost 30 km past the bed (Noren et al.,1999). Noren et al (1999) attribute this dramatic reduction to high turbulence and the lack of stratification. Asmus and Asmus (1991) found less dramatic reductions in phytoplankton biomass of 37 % by mussel beds in a more stratified area of the German Wadden Sea. Generally though, a more intense impact would be expected where when mixing is lower.

Phytoplankton community structure may also change during passage over a mussel bed. Noren et al (1999) reported an increase in the concentration of cells 2 to 12 μm in diameter and a decrease in the concentrations of dinoflagellates in the vicinity of mussel beds. They (Noren et al., 1999) suggest that faster growing algae might dominate the plankton community over a mussel bed if there is no resource limitation. This might also occur at mussel farms.

Depending on the physical characteristics of their environment, mussel populations may even have the capacity to utilize excess primary production stimulated by their own excretory products or by other inputs such as excess anthropogenic nitrogen (Cloern, 1982; Loo and Rosenberg, 1989). In an area of the Kattegat which receives large inputs of nitrogen from rivers, the bivalves *Cardium edule* and *Mya arenia* consume more than 90% of the seston while the net zooplankton community consume only ca. 10 % (Loo and Rosenberg, 1989). Competition for bloom-forming food species may arise where zooplankton development lags behind a bloom and bivalves, able to survive long periods of low food availability, are present in high biomass and able to more fully utilize a bloom. Loo and Rosenberg (1989) suggest that long residence times and high rates of re-suspension allow benthic suspension feeders to control phytoplankton biomass in shallow water bodies such as the Kattegat. As mussels are cultured in the water column on long lines in Notre Dame Bay, resuspension from the bottom may be less important in the efficiency of their utilization of phytoplankton. However, factors such as residence time

are probably still important in determining the degree of reduction in seston by farmed mussels.

1.5 Seston depletion and nutrient cycling by cultured mussels

The feeding activities and excretion of ammonia by cultured mussels can also lower the autotrophic biomass and raise or lower the levels of certain nutrients such as ammonia. This has been shown in a variety of environments including colder environments such as Dutch estuaries (Dame et al 1991; Dankers et al. 1995), and coastal Ireland (Rodhouse et al. 1985) as well as warmer environments such as Mediterranean lagoons (Souchu et al., 2001) and coastal New Zealand (Ogilvie et al., 2000). In coastal Ireland, for example, farmed mussels can clear 47% of the chlorophyll and 62% of the carotenoids over a tidal cycle (Rodhouse et al. 1985). In a lagoon in the Mediterranean, which has a long residence time and low tidal range, chlorophyll and POC concentrations were 44% and 27% lower, respectively, in a mussel and oyster farm compared to a nearby reference site (Souchu et al., 2001). At the same time, ammonia, phosphate and silicate were 73%, 36% and 20% higher respectively in the farm compared to the reference site (Souchu et al., 2001).

Any effects of mussel farms on phytoplankton and nutrients may vary as a function of seasonally-changing feeding activities of the bivalves. The clearance rates of *M. edulis*

and *P. magellanicus* in a cold water, Canadian environment may be twice as high in October and November as at other times of year, as a function of both food quantity and quality and of physiological regulation of feeding and digestion (Cranford and Hill, 1999). Higher clearance rates are generally coupled with higher ammonia excretion rates (Bayne and Scullard, 1977). Therefore any effects of mussel farming on zooplankton communities may be seasonal as well.

The seasonal effect of mussels on phytoplankton has been studied in New Zealand where *Perna canaliculus* may reduce phytoplankton biomass during autumn and winter, while during spring, phytoplankton abundance is higher inside the farms than outside, causing the local ecosystem to be a net producer of oxygen (Ogilvie et al., 2000). Effects on water chemistry were also seasonal. There was no overall difference between farm and reference sites but during the spring bloom water column ammonia concentrations were three times higher in the farm than in the reference site (10.7 vs. 3.1 mmol m^{-2}, respectively).

The higher sedimentation rates under mussel ropes and the possible concurrent changes in sediment chemistry and sediment -water chemical fluxes may also affect the pelagic system, especially during resuspension events. Resuspension may add a pulse of both nutrients and phytoplankton from the near-bottom zone into the water column. In

microcosms simulating the Southern Baltic, typical resuspension rates had a negative effect on ciliates while the growth of pico- and nanoautotrophs and bacteria were positively affected (Garstecki, Wickham, and Arndt, 2002). These changes in the microbial food web may then affect the "higher" food web. Work by Baudinet et al. (1990) indicates that mussel biodeposits may lead to eutrophication characterized by altered ratios of nutrients such as ammonia, nitrate and silicate which may result in changes in the taxonomic composition of the phytoplankton as discussed previously.

In some areas, mussel ropes may also include a large population of epifauna which may also interact with the pelagic ecosystem. For example, in the Mediterranean Sea, oyster farms may be fouled by a community consisting of macroalgae, bryozoans, ascidians and polychaetes, all of which may affect the fluxes of nitrogen and oxygen (Mazouni, Gaertner, and Deslous-Paoli, 1998). There have been few studies of particle ingestion by the epifaunal community but presumably where organisms such as the ascidian *Ciona* sp. are abundant they may also exert a grazing effect on the autotrophic community. Thus, a study of the effects of mussel farming on the pelagic community may in some cases be a study of the total effect of a community of animals, not just of mussels themselves. Fortunately, the mussel farms in Newfoundland do not have problem with fouling by tunicates (or other filtering animals) such as occurs in other parts of Atlantic Canada (http://www.glf.dfo-mpo.gc.ca/sci-sci/inva-enva/index-e.html). Therefore the mussels are

probably the main consumers of plankton in the system and as such observations of potential impacts are not confounded by biofouling.

1.6 Other evidence suggesting potential impact of mussels on zooplankton

Mesocosm studies illustrate how the presence of mussels may affect the taxonomic composition of the community in addition to the concentration of photosynthetic pigments in the water column. However, as with any mesocosm experiments the short duration, size of system and wall effects must be considered when interpreting the results. In mesocosm experiments performed by Prins et al (1995), phytoplankton biomass was reduced in mesocosms with the highest biomass of mussels and composed of a higher proportion of diatoms than those without. Specifically, there was a decrease in the concentration of *Phaeocystis* sp. and an increase in microflagellates. The diatom *Rhizosolenia* sp. was replaced by mixtures of *Asterionella glacialis*, small *Chaetoceros* species, *Nitzschia deliicatissmia* and *Cerataulina bergonii.* Phytoplankton growth rates were highest in mesocosms with higher mussel biomass, most likely due to increased supply rates of ammonium.

Horsted and colleagues (1988) found lower biomass of *Tintinnopsis* spp. and *Synchaeta* spp. in mesocosm enclosures with mussels but no affect on the abundance or biomass of *Acartia tonsa*. The duration of the experiments may have been too short to have resulted

in a change in the latter taxon. Their work also illustrates the feedbacks between mussel grazing and regeneration of primary production by excreted ammonia. Addition of similar concentrations of nutrients alone raised phytoplankton biomass to 256% of controls while biomass was reduced to 10 to 59% of control levels with the addition of various levels of mussel biomass (Horsted et al., 1988). The phytoplankton community composition was also affected with 70-93% picoplankton in enclosures with mussels but only 4 to 20% in mussel-free controls.

While mussels may reject some particles into pseudofaeces (Kiorbe and Mohlenberg, 1981) they are thought to filter from suspension essentially 100% of those particles larger than ca. 4 μm (Mohlenberg and Riisgard, 1978) regularly utilizing particles up to 110 μm in size (Newell et al, 1989). Zooplankton populations may thus be affected through the direct ingestion of their adult or juvenile stages by mussels. Davenport et al. (2000) found nauplii of the copepod *Temora longicornis*, cladocerans such as *Podon* sp., gammarid amphipods and rotifers up to 6 mm in length in the guts of *Mytilus edulis*. Animals that were not ingested but bound in pseudofaeces were either killed or made moribund. Bivalve larvae, on the other hand, ingest particles in the 15 to 25 μm range and therefore likely have less impact on zooplankton populations (Raby et al., 1997).

1.7 Summary and thesis outline

Mussel farms have the potential to affect the benthic and pelagic ecosystems of the coastal areas in which they are situated. Like natural mussel beds, they may affect nutrient cycling and concentration, and the biomass, size structure and community composition of autotrophic and heterotrophic communities. Zooplankton may be affected indirectly through changes in species composition of the microplankton or directly through competition with or ingestion by mussels. These effects may be species-specific.

The possible ecosystem interactions of mussel farming and the feedbacks between ecosystem effects and mussel productivity may be important in estimating carrying capacity of an area and may therefore be important considerations in husbandry practices (Smaal, et al., 2001). Possible changes in coastal zooplankton communities are important in the coastal ecosystem management context as zooplankton are an important step in the trophic transfer of energy from lower levels in the food web to organisms like fish (Mallin and Paerl, 1994).

This thesis presents data on the zooplankton community of two mussel farms and their references sites in Notre Dame Bay examined in a quarterly study in 2001 and 2002. In Chapter 2, the abundance, biomass and community composition of the zooplankton of the farms are compared to those of the reference sites. Physical data is presented which

justifies the comparison of each farm with its reference site. In Chapter 3 the zooplankton size distributions of the farms and reference sites are compared. Chapter 4 summarizes what this study indicates about the factors controlling zooplankton community characteristics in coastal Newfoundland inlets.

Chapter 2: Effect of mussel farming on zooplankton community characteristics in Notre Dame Bay, Newfoundland

2.1 Introduction

While benthic impacts of bivalve aquaculture have been well studied (see Kaiser et al., 1998 and references therein) pelagic effects have received little attention except for reports of reductions in seston levels and the subsequent feedbacks on bivalve production. Evidence from studies of natural mussel communities and experimental mesocosms indicates impacts on the composition and size structure of pelagic ecosystems mediated through mussel feeding and excretion of ammonia (Asmus and Asmus, 1991; Horsted et al, 1988, Prins et al, 1995). Generally, the presence of mussels and other bivalves is associated with declines in the standing biomass of autotrophs, despite sometimes higher rates of production and changes in autotrophic community composition with a higher abundance of smaller, faster growing species and a decline in the abundance of dinoflagellates.

There has been little work on the effect of suspension feeding bivalves on zooplankton communities. Potential avenues of impact include direct ingestion of zooplankton adults or juvenile stages (Davenport et al., 2000), competition for common food particles and bivalve- induced changes in the concentration and composition of the phytoplankton. There has been no published examination of the impact of mussel farms on the naturally occurring zooplankton community.

Determination of the impact of bivalves on the pelagic system may be confounded by the seasonal cycles of ingestion and excretion rates of the mussels (Cranford and Hill, 1999)

and the abundance and biomass of zooplankton. These cycles are likely not in phase and are functions of environmental forcing which varies on seasonal and interannual time scales. This study assesses the impact of mussel farms on the zooplankton community of two inlets in Notre Dame Bay, Newfoundland. Zooplankton community characteristics of the mussel farms are compared to those of two nearby inlets without farms. An impact is assumed to exist where there is a significant difference between the farms and references. Field work was conducted quarterly in the farms and nearby reference sites over an annual cycle in 2001/2002. This work is also one of the first to describe the zooplankton community structure of inshore Newfoundland waters.

2.2 Materials and Methods

2.2.1 Study sites

The study sites were two mussel farms (Black Gold, Inc., Charles Arm and Atlantic Ocean Farms, Fotune Harbour) and their companion reference sites in Notre Dame Bay, Newfoundland. For the remainder of this report these locations will be referred to as the Charles Arm farm (CA farm), the Saunders Cove reference site (CA ref), the Fortune Harbour farm in the northwest arm (FH farm) and the Fortune Harbour reference site in the southeast arm (FH ref) (Fig. 2.1 a-c). Given the very small human population immediately surrounding both sites and the lack of industry (Statistics Canada) these inlets are relatively free from anthropogenic pollution. According to the operators, during the time of the study the biomass of mussels in Charles Arm was approximately $2.0*10^5$ kg (Mills, personal communication) and in Fortune Harbour Farm was approximately $1.5*10^5$ kg (Wiseman, personal communication).

The physical attributes of the farms have been the subject of study during the development of the aquaculture industry in Newfoundland (Clemens et al, 2000). Surface temperatures in this area range from summer highs of 18 °C to winter lows approaching -2 °C. Salinities are generally over 27 psu except during spring runoff when salinity at 2 m approaches 17 psu. Both sites are ice covered in winter.

The axial length of Charles Arm is approximately 3.0 km with a width of 200- 500 m and a maximum depth of approximately 20 m. The area of Charles Arm is 0.59 km^2. The axial length of FH farm is ~2.5 km with a width of ~ 400 m along most of its length except for a narrow point of less than 100 m. The farm covers approximately 80% of the area of the inlet (1.1 km^2) and has a maximum depth of approximately 35 m. Longlines stretch from shore to shore at both farms. The areal biomass of mussels at Charles Arm is ca. 2.5-times higher than that at Fortune Harbour (3.4×10^5 kg km^{-2} vs. 1.4×10^5 kg km^{-2}, respectively).

The currents at both farms are weak with minima of< 2 cm s^{-1} at the heads of both farms and maxima of 5-10 cm s^{-1} and 3 cm s^{-1} at the mouths of Charles Arm and Fortune Harbour, respectively (Coffin 2001; Timko, de Young, and Foley 1999). Charles Arm flushes 1-2.75 times per week (Penney et al 2001). The tidal ranges are 0.75 m at Charles Arm (Penney et al 2001) and 0.92 m at Fortune Harbour (Coffin 2001). Charles Arm has very little freshwater input and tidal exchange is the dominant source of water movement (Penney et al 2001).

At both sites chlorophyll a concentrations routinely reach ~5 μg L^{-1} during phytoplankton blooms (Clemens et al 2000; Coffin 2001).With respect to composition of the phytoplankton, Charles Arm is the better studied of the two farms. For most of the year the phytoplankton community of Charles Arm is dominated by small (2-20 μm diameter)

diatoms and autotrophic nanoflagellates (Penney et al 2001). The fall bloom is dominated by the diatom *Skeletonema costatum,* while the spring bloom consists mostly of the autotrophic nanoflagellates *Micromonas* spp. and *Pyramimonas* spp. and the diatoms *Chaetoceros* spp. and *Fragilariopsis* spp. (Penney et al 2001). During winter, food quality may be low due to low phytoplankton: detritus ratios (Penney et al 2001).

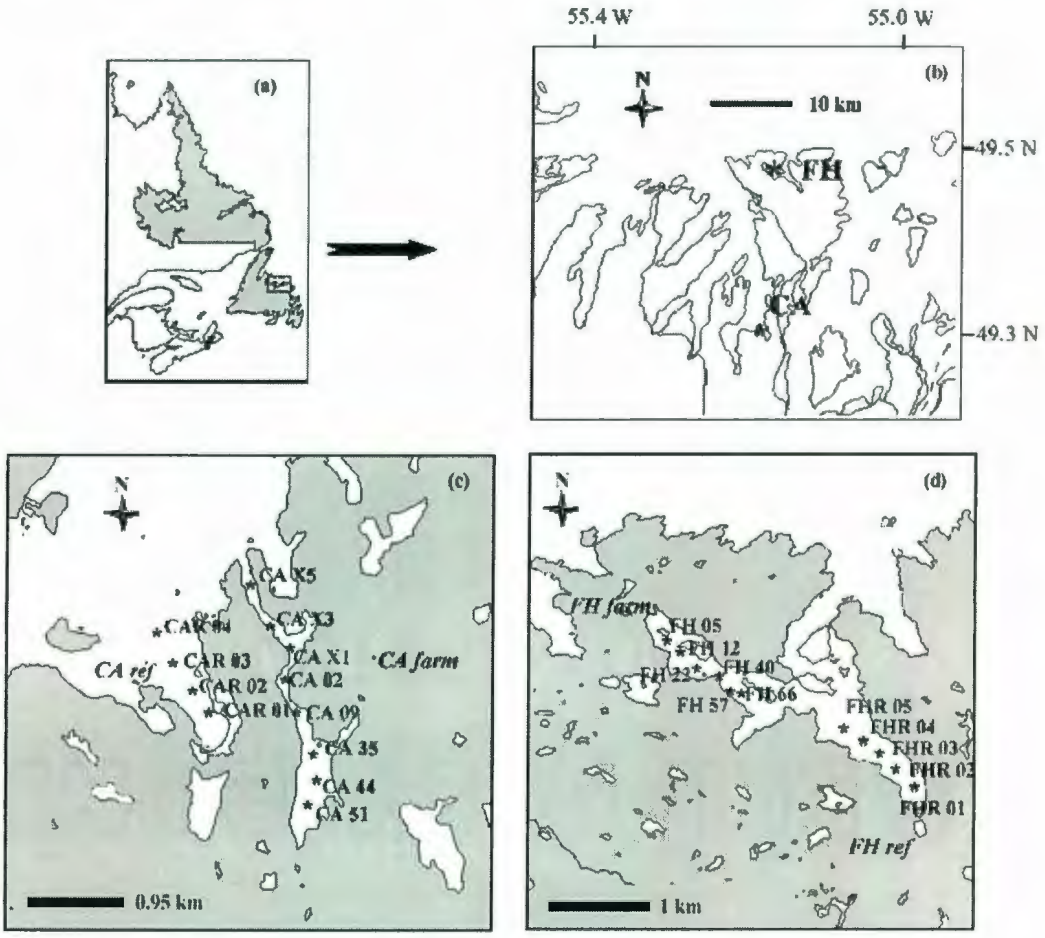

Figure 2.1(a-c): Study sites in Notre Dame Bay Newfoundland a) Sites in relation to Newfoundland; b)Sites in relation to each other and Notre Dame Bay; c) stations in Charles Arm farm and reference and d) Stations in Fortune Harbour farm and reference. Maps were compiled using AquaGis software. (www.aquagis.com)

2.2.2 Methods

2.2.2.1 Field collection

Zooplankton samples were collected using vertical net tows at three to six stations at each farm and reference site in August and November of 2001, and March and July of 2002 (Table 2.1; for station locations see Figure 2.1). A 50-cm diameter ring frame was fitted with a 110-μm mesh net measuring 2.5 m long. The net was equipped with an inside and outside flowmeter to monitor distance traveled and clogging. Triplicate samples were collected at each station. Two were fixed in 500-ml jars in 70-90 % ethanol for determination of mean abundance and the other frozen fresh in 100-ml jars for later determination of biomass . Samples were collected at each farm and its reference site on successive days at the same time and tidal stage. A CTD cast was made at each station with a Seabird SBE 25 except during March 2002, when through-ice sampling necessitated the use of a smaller SBE19. The SBE25 had a photosynthetically active radiation (PAR) sensor, in situ flourometer and dissolved oxygen (DO) sensor, while the SBE19 did not have a fluorometer or DO sensor.

Table 2.1: List of stations sampled at each sampling period in 2001 and 2002 (for approximate station locations see Figure 2.1)

Sampling Period	Charles Arm stations (CA)	Saunders Cove stations (CA ref)	Fortune Harbour farm stations (FH)	Fortune Harbour reference stations (FH ref)
08/2001	09, 51, **44**, 02, **X1**, **X3**,	**01**, **02**, **03**, 04	12, **05**, **22**, 40, **57**,	**01**, **02**, 03, **04**, 05
10/2001	**44**, **35**, 02, **X3**	**01**, **02**, 03, **04**	**05**, **22**, **40**, 57	01, **02**, **03**, **04**
03/2002	**51**, **44**, **35**	not sampled	**05**, **22** 57, **66**	**01**, **03**, **05**
06/2002	**51**, 44, **35**, **X1**, X3	01, **02**, 03, **04**, **05**	**05**, 22, 40, **57**, **66**	01, **02**, **03**, 04, **05**

2.2.2.2 Preserved Sample Processing

Samples were returned to the Ocean Sciences Centre, Memorial University, for storage and processing. Within two to three weeks of return samples were removed from alcohol and split in half with a Folsom splitter. One of the splits was transferred to 4% buffered formaldehyde and used later for species identification. The other split was sieved through 500 μm and then 80 μm mesh. The greater than 500μm fraction (hereafter referred to as the large animal fraction) was transferred to 4% buffered formalin to be used for image analysis of large animal size distributions. The small animal fraction was then transferred to filtered sea water from Logy Bay, Newfoundland and used for Coulter Counter Multisizer II® counts and analysis of size distributions.

2.2.2.3 Biomass

Frozen samples were returned to the Ocean Sciences Centre and kept at -20 °C until analysis. They were thawed at 5 °C and suspended in (1μm) filtered sea water from Logy Bay, Newfoundland. Measured aliquots were filtered onto pre-ashed, pre-weighed GF/C filters. Each sample was washed with distilled water in a ratio of 5mL distilled water for every 200mL SW used. The filters were then lyophilized at -60 °C overnight brought to room temperature and weighed. Using this method, any small amounts of remainig salt adhere to the edges of the container in which the samples are lyophilized.

2.2.2.4 Community composition

Samples from three stations were chosen at random from all stations sampled each farm and reference site for each of the time periods following a computer-generated list of random numbers. Measured aliquots of formalin-preserved splits of the samples were taken with a Stempel pipette and the animals identified under a Wild® dissecting scope. Enough aliquots were counted to reach counts of at least forty individuals for each of the major taxa and whole samples were sometimes counted for enumeration of rare species. Usually ~500 animals were identified and counted from each split. References used for identification included Todd and Laverick (1991), Newell and Newell, (1977) and the ICES zooplankton identification leaflets.

2.2.2.5 Abundance estimates

The number of animals (<500 μm) counted with the Coulter Counter Multisizer II® (fitted with a 560 μm orifice tube) was used to compute the abundance of small animals, while the number of animals counted by image analysis was used to compute the abundance of large animals. See Chapter 3 for a full explanation of sizing procedures. Estimates of abundance obtained from microscopic community composition enumerations were compared with the estimates of abundance obtained during size estimation using the Coulter Counter and image analysis and were found to be statistically indistinguishable (pairwise t-test, $n=44$, $t=-11.91$ $p<0.01$).

2.2.2.6 Statistical analysis

Mutivariate analysis of community composition was used as a means of characterizing general patterns in zooplankton community structure in Notre Dame Bay. Cluster analysis and principle components analysis was conducted using the MSVP v.3.13d (Kovach Computing Services) statistical package. Abundance data from the community composition enumerations (for stations used see Table 2.1) were log + 1 transformed prior to multivariate analysis to prevent the more consistently abundant taxa from swamping the analysis. Cluster analysis of stations was performed on the Bray-Curtis dissimilarity matrix with the Unweighted Pair Group Method with Arithmatic

Mean (UPGMA) clustering method. Principle components analysis was also conducted to separate stations based on the major species composition.

General linear modeling was used to analyze the individual species abundance, size fractionated abundance and biomass as in the following:

$$\text{Response variable} = \beta_0 + \beta_{\text{Season}}\,\text{Season} + \beta_{\text{Location}}\,\text{Location} + \beta_{\text{Site}}\,\text{Site} + \beta_{\text{Distance}}\,\text{Distance} + \beta_{\text{Location*Site}}\,\text{Location*Site} + \beta_{\text{Season*Site}}\,\text{Season*Site} + \beta_{\text{Season*Location}}\,\text{Season*Location} + \varepsilon$$

Where

Response variable is $N_{\text{species X}}$, N_{small}, N_{large}, or Biomass

Season is August 2001, November 2001, March 2002 and July 2002

Location is location in Notre Dame Bay (CA or FH)

Site is farm or reference

Distance is the distance of each station from the head of the site

Assumptions for this analysis were examined by checking plots of residuals versus fits for homogeneity and independence of the variance.

2.2.2.7 Power analysis

Where "Location" and "Site" explanatory variables were not significant in the general linear model described above, the difference between the two sites or locations was increased by adding a percentage of the mean to all values in one location or site until a significant difference was found using in the following two models:

$$\text{Response variable} = \beta_0 + \beta_{\text{Location}} \text{Location} + \varepsilon$$

$$\text{Response Variable} = \beta_0 + \beta_{\text{Site}} \text{Site} + \varepsilon$$

2.3 Results

2.3.1 Physical characteristics of the sites during sampling

Figures 2.2 (a-b) to 2.16 (a-b) show the temperature and density profiles along the sampling transects. Each variable is placed on the same scale for all four study areas in each time period. Over all sites and locations, salinities ranged between 29 and 32 psu. Oxygen levels were consistently higher than 5 ml l^{-1} at all depths and were therefore probably not limiting for zooplankton (Stalder and Marcus, 1997). There was a notable absence of a strong horizontal salinity gradient over the study period.

In August 2001 surface and bottom temperatures were ~17 and ~ 7 °C, respectively at the CA sites and ~13 and 5 °C, respectively at the FH sites. However, temperature stratification calculated as the mean difference between surface and bottom waters at all stations was higher in FH than in CA (Table 2.1). The degree of stratification was lower at all sites in November compared to August 2001, with CA less strongly stratified as it was in August (Tale 2.1) Surface and bottom temperatures were ~7 and 5.1 °C, respectively in CA sites and 5 and 2 °C, respectively in the FH sites.

Sampling in March 2002 was through land fast ice. The water column was relatively homogeneous in terms of temperature, salinity, and density with temperature of ca -1 °C (Table 2.1). Sampling in CA ref was impossible at this time of year due to insufficient

ice strength. Thermal stratification was strong again in July 2002, with the largest differences between surface and bottom waters at the FH sites, as was true in 2001 (Table 2.2)

Table 2.2: Mean difference between highest and lowest density (σ_t) salinity (psu) and temperature (°C) for each of the sites studied during each time period. The mean difference is the mean of three to six stations. The standard deviation of density is in parentheses.The stations used to compile these means can be found in Table 2.1.

	CA	CA ref	FH	FH ref
August				
temperature	3.9	2.9	9.6	10.1
density	1.2	1.0	2.5	2.5
	(0.8)	(0.7)	(1.5)	(1.6)
November				
temperature	0.4	0.1	2.2	3.1
density	0.3	0.1	0.8	0.9
	(0.3)	(0.03)	(0.8)	(0.8)
March				
temperature	0.2	Not	0.3	0.3
density	0.3	sampled	0.2	0.1
	(0.2)		(0.03)	(0.2)
July				
temperature	4.8	5.0	9.4	6.5
density	1.1	1.1	2.6	1.7
	(0.4)	(0.4)	(1.8)	(0.4)

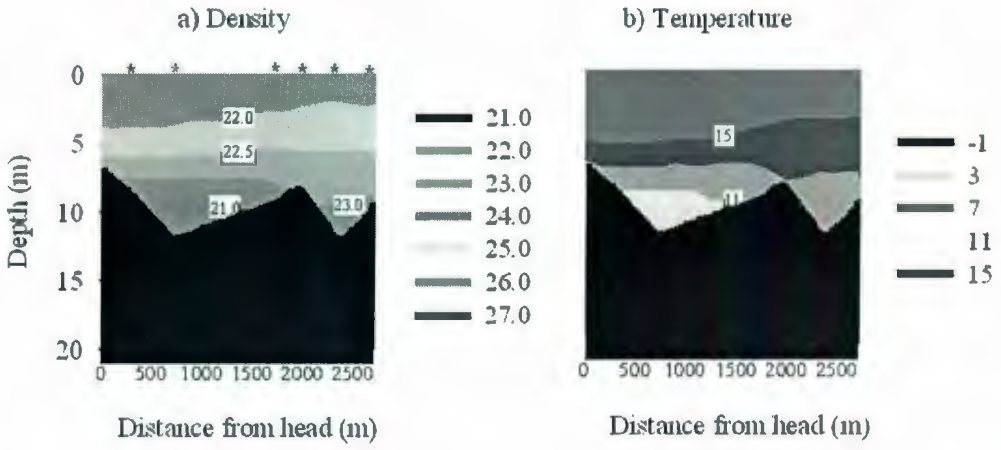

Figure 2.2 (a-b): Density and temperature contour plots of Charles Arm (farm) and reference during August 2001 sampling. The bottom contour is shown in black. For this and the following physical data figures density is measured as σ_t and temperature as $^{\circ}C$. The asterisks indicate sampling locations.

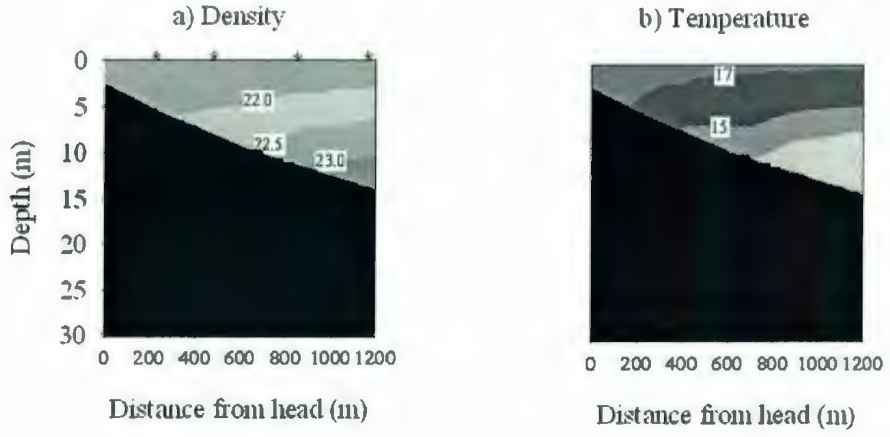

Figure 2.3 (a-b): Physical characteristics of CA ref during August 2001 sampling

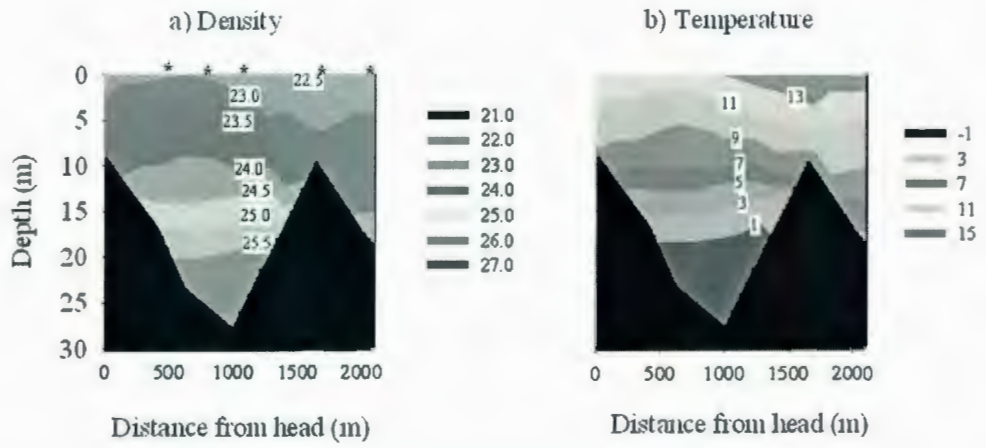

Figure 2.4 (a-b) Physical characteristics of FH farm during sampling in August 2001

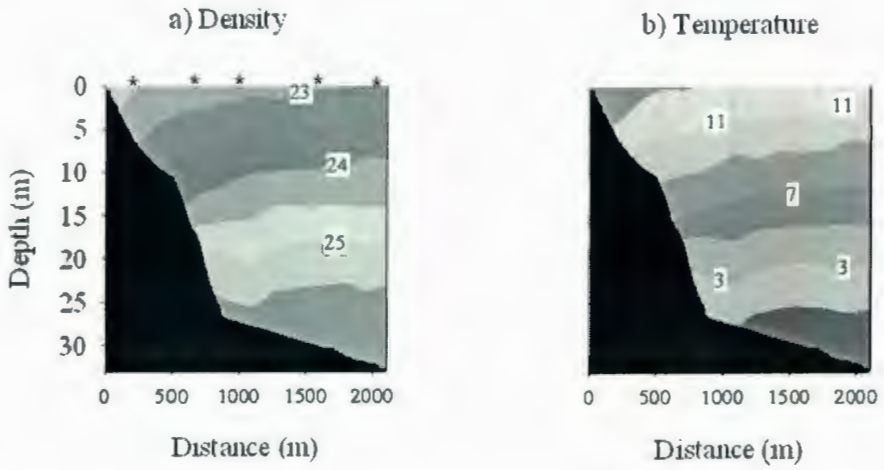

Figure 2.5 (a-b): Physical characteristics of FH reference during August 2001

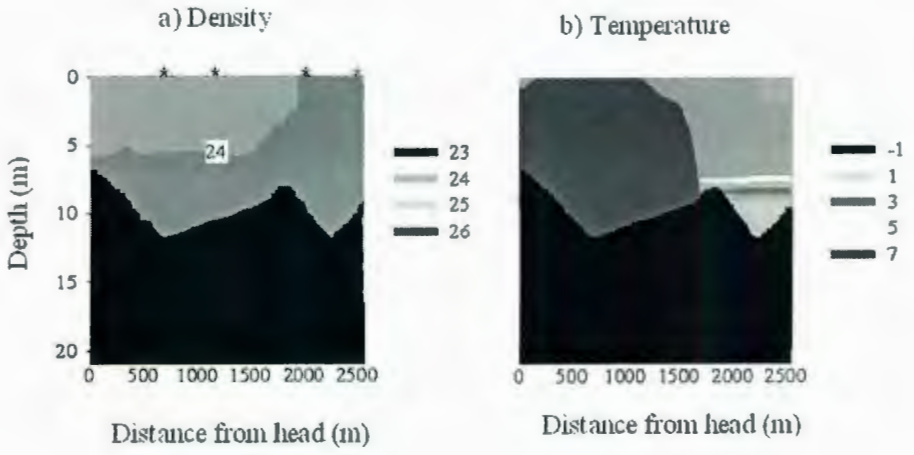

Figure 2.6 (a-b): Physical characteristics of CA farm during November 2001 sampling

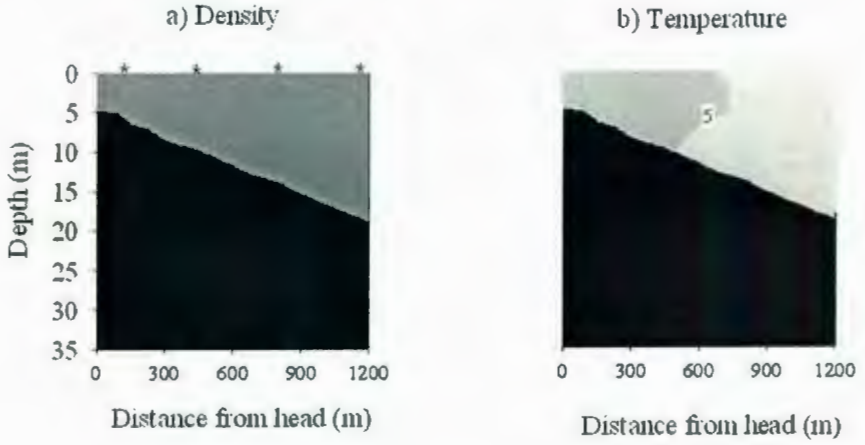

Figure 2.7 (a-b): Physical characteristics of CA reference during November 2001 sampling

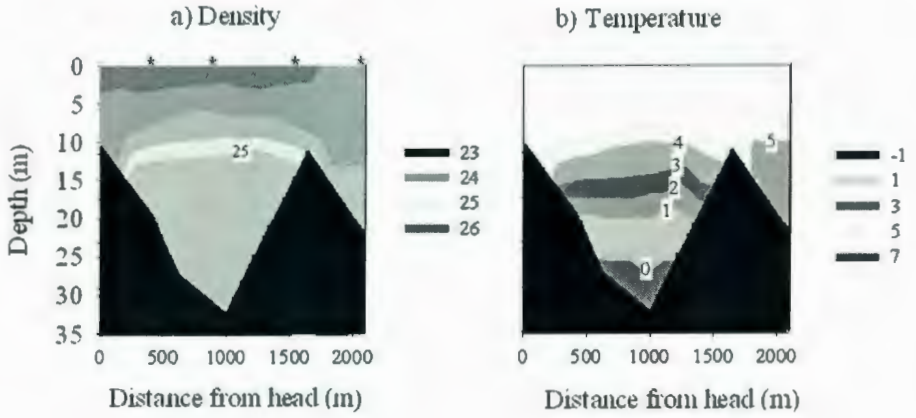

Figure 2.8 (a-b): Physical characteristics of FH farm during November 2001 sampling

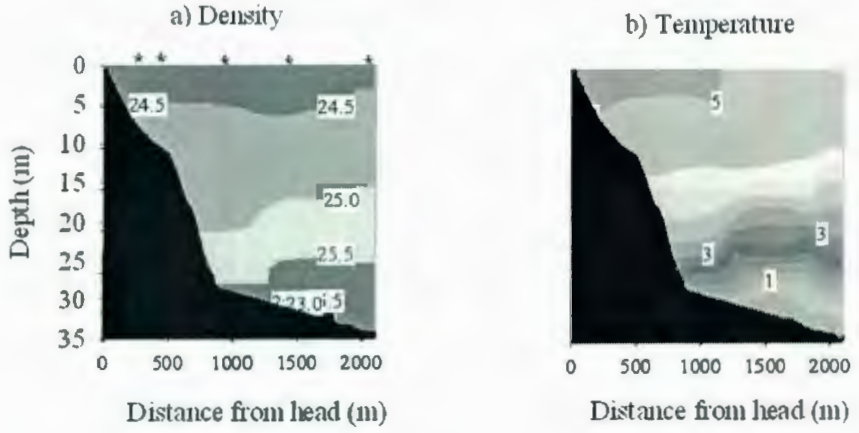

Figure 2.9 (a-b): Physical characteristics of FH ref during November 2001 sampling

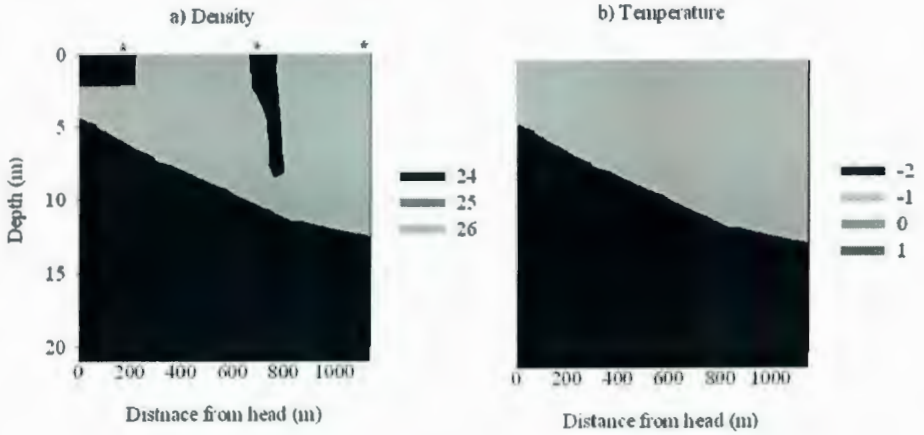

Figure 2.10 (a-b): Physical characteristics of CA farm during March 2002 sampling

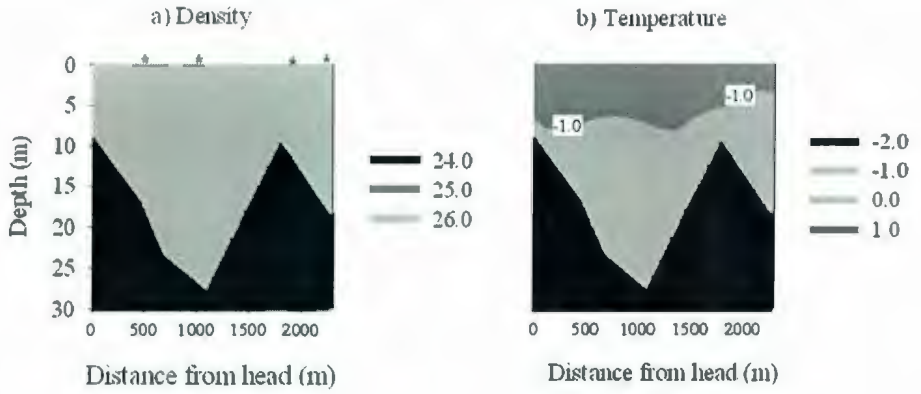

Figure 2.11 (a-b): Physical characteristics of FH farm during March 2002 sampling

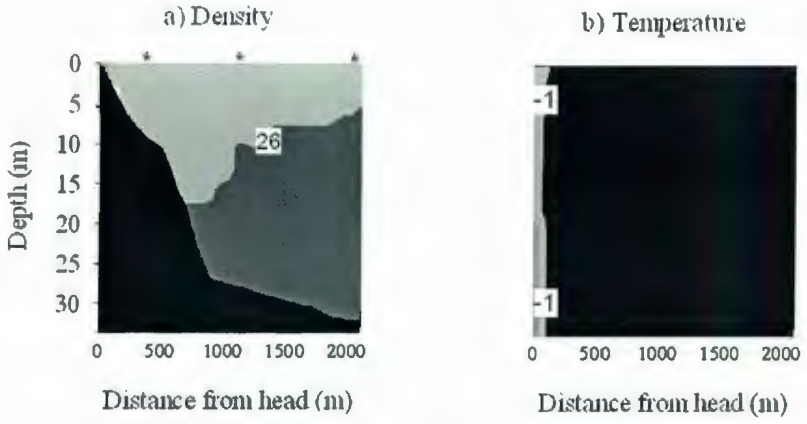

Figure 2.12 (a-b): Physical characteristics of FH ref during March 2002 sampling

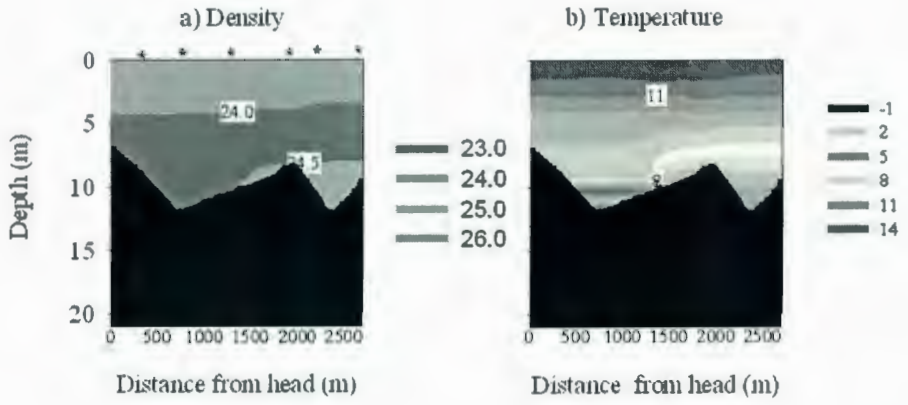

Figure 2.13 (a-d): Physical characteristics of CA farm during July 2002 sampling

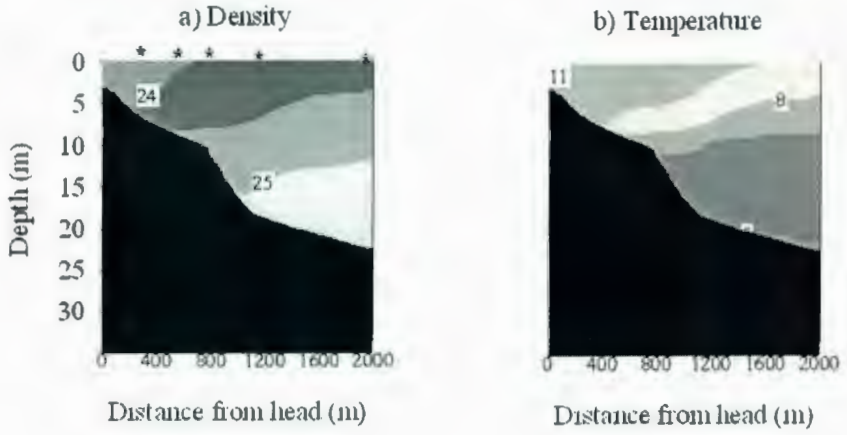

Figure 2.14 (a-b): Physical characteristics of CA ref during July 2002 sampling

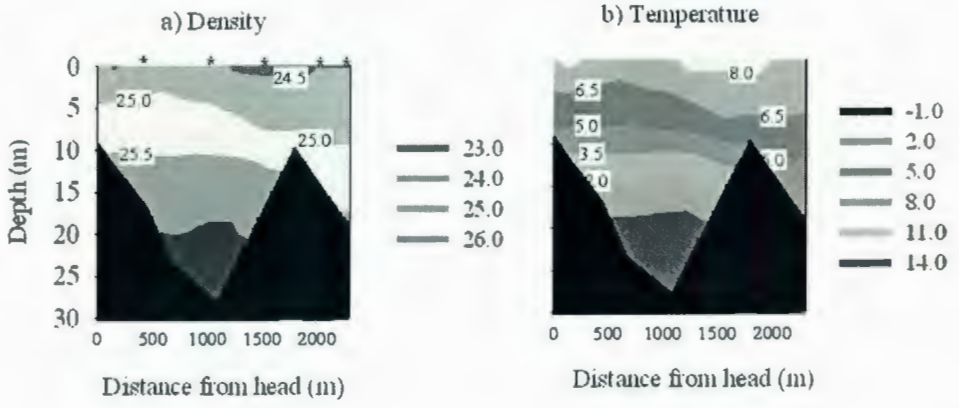

Figure 2.15 (a-b): Physical characteristics of FH farm during July 2002 sampling

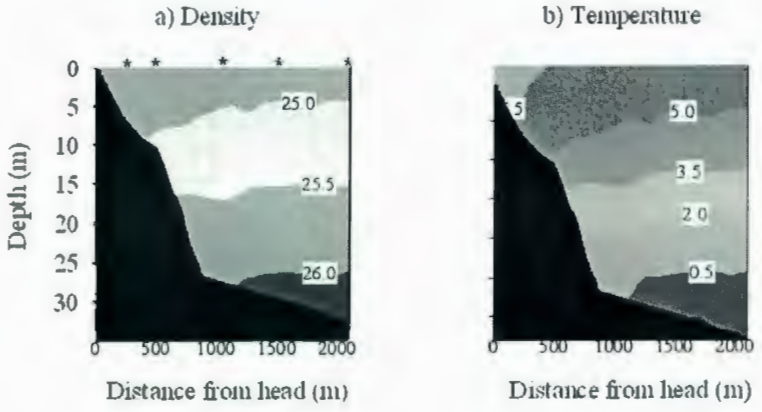

Figure 2.16 (a-b): Physical characteristics of FH ref during July 2002 sampling

2.3.2 General community composition

As shown in Figures 2.17 to 2.20, (Table 2.2) four or five species dominated the zooplankton community at all sites in Notre Dame Bay in all seasons i.e., *Acartia* sp., *Oithona* sp., *Temora* sp. and *Pseudocalanus* sp. Meroplankters were generally rare. In addition to the common species, medusae including *Obelia* sp., and *Aurelia aurita* were present in the size range studied in all sites in August 2001 and July 2002 (and to a lesser extent in November 2001) but these are not included in the study as they were not routinely captured in our net. A small number of *Calanus finmarchic*us were present at the sites in July 2002. Siphonophore cormidia were present in FH in November 2001 and March 2002. CA farm samples contained large centric diatoms and mussel faecal pellets in March, even though most of the sites were ice covered. *Mytilus* veligers were abundant at all sites in July 2002, especially so at the farms.

Cluster (Figure 2.21) and principle components analyses (Figure 2.22 and 2.23) did not reveal a clearer association of stations based on the presence or absence of a mussel farm. This analysis did separate warmer-water summer assemblages dominated by *Acartia*, *Temora*, copepod nauplii and *Centropages* from colder-water assemblages dominated by *Oithona*, *Pseudocalanus*, harpacticoid copepods and polychaete larvae. This is seen as a clustering of summer samples and separate clusters of November and March stations in Figure 2.21 as a concentration in the lower right of the PC plot with March samples

falling the upper left of the PC plot and November samples falling in the middle. This follows the seasonal pattern of increased densities and decreased temperatures in November and March compared to July and August. Salinity variations are not consistent with this pattern, being slightly higher in March and July and lower in August and November.

Log + 1 abundance of *Acartia* (r^2=47%, p=0.0001, df=44), *Temora* (r^2=57%, p=0.0001, df=45) large animal abundance (r^2=33%, p=0.0001, df=44) copepod nauplii (r^2=45%, p=0.0001, df=45) and small animal abundance (r^2=32%, p=0.030, df=44) were strongly correlated with temperature. The abundance of harpacticoid copepods (r^2=13%, p=0.016, df=44), *Centropages* (r^2=15%, p=0.009, df=44) and *Pseudocalanus* (r^2=21%, p=0.002. df=44) were significantly but less strongly correlated with temperature.

Table 2.3 List of zooplankton taxa observed in the study

Phylum Cnidaria
- Class Hydrozoa
  - Order Siphonophora unidentified cormidia
  - Order Hydroida
    - Suborder Leptomedusae
    - *Obelia* sp.
- Class Scyphozoa
  - Order Semaeostomae
    - *Aurelia aurita*
    - *Cyanea* sp. (not enumerated but observed)

Phylum Arthropoda
- Sub-phylum Crustacea
- Class Copepoda
  - Order Calanoida, Sars, 1903
    - Family Acartidae, Sars, 1908
      - *Acartia longiremis,* Lilljeborg, 1853
    - Family Temoridae, Giesbrecht, 1889
      - *Temora longicornis*, Muller, 1792
    - Family Clausocalinidae, Giesbrecht, 1873
      - *Pseudocalanus* sp.
    - Family Centropagidae Giesbrecht, 1892
      - *Centropages hamatus* Lilljeborg, 1853
    - Family Calinidae
      - *Calanus finmarchicus*
  - Order Harpacticoida, Sars, 1903
    - *Microstella norwegica*
    - *Tisbe* sp.
  - Order Cyclopida
    - *Oithona* sp.

- Class Maxillopoda
  - Subclass Cirripedia unidentified nauplii

- Class Branchipoda
  - Order Cladocera
    - *Podon* sp.
    - *Evadne nomanni*

- Class Malacostraca
  - Order Mysida 1 unidentified species
  - Order Amphipoda 1 unidentified species
  - Order Decapoda 1 unidentified crab zoae

Table 2.2 continued: List of zooplankton taxa observed in the study

Phylum Chaetognatha
- Order Aphrahmophora
  - *Parasaggita sp.*

Phylum Echinodermata
- Subphylum Eleutherozoa
  - Class Asteroidea unidentified larvae
  - Class Echinoidea unidentified larvae

Phylum Chordata
- Subphylum Urochordata
  - Class Appendicularia
    - *Fritillaria borealis*
    - *Oikopleura* sp.

Phylum Annelida
- Class Polychaeta Grube, 1850
  - Order Capitellida unidentified larvae
  - Order Spionida unidentified larvae

Phylum Mollusca
- Class Bivalvia
  - Order Anasomyaria
    - Family Mytiladae
      - *Mytilus edulis* Linnaeus larvae
  - Class Gastropoda
    - Order Mesogastropoda
      - Family Littorinidae
      - *Littorina* sp.

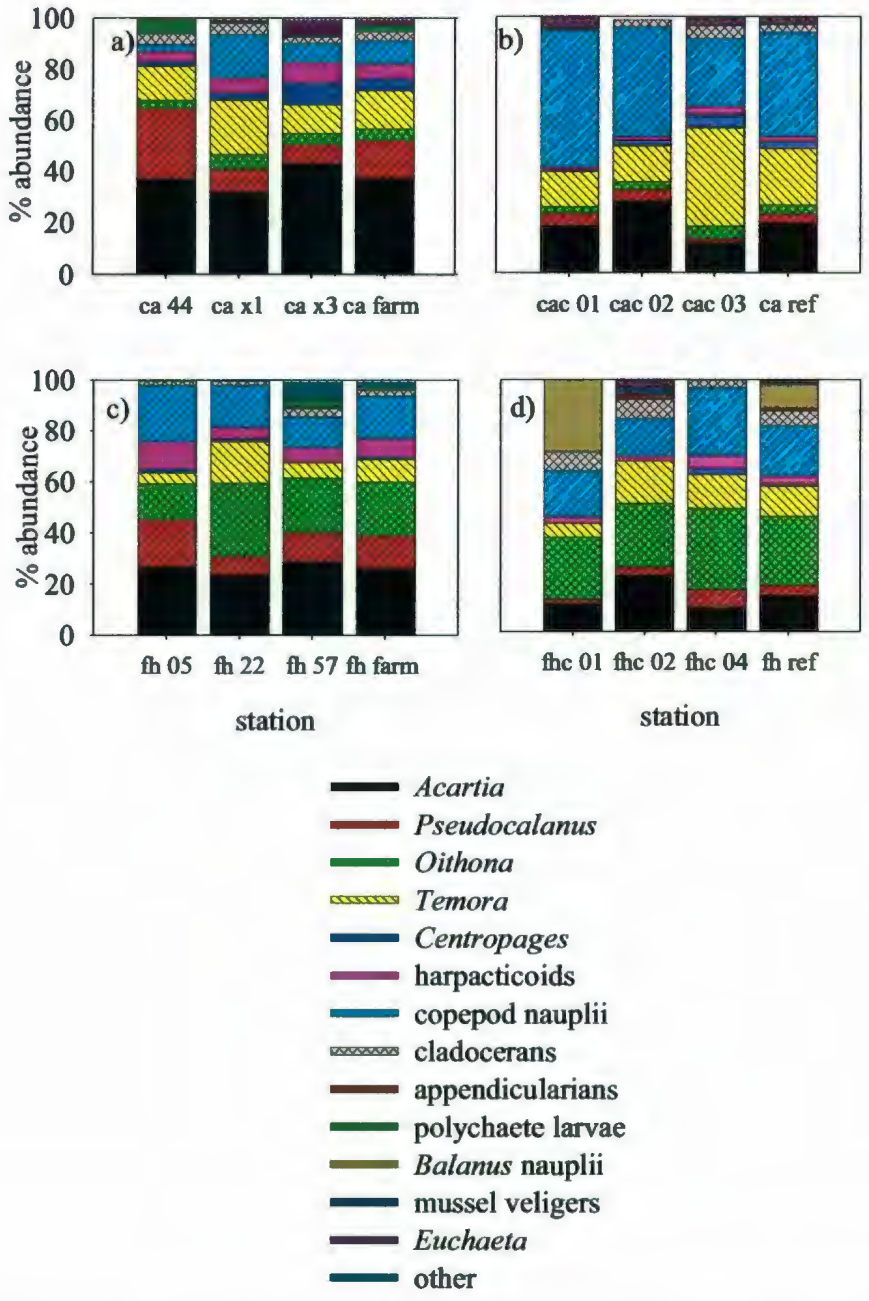

Figure 2.17 (a-d): Zooplankton community composition in August 2001 for a) CA farm, b) CA ref, c) FH farm and d)FH ref. The first three bars in each panel represent the mean composition(of two tows) of stations within each area and the fourth bar is the mean of the first three.

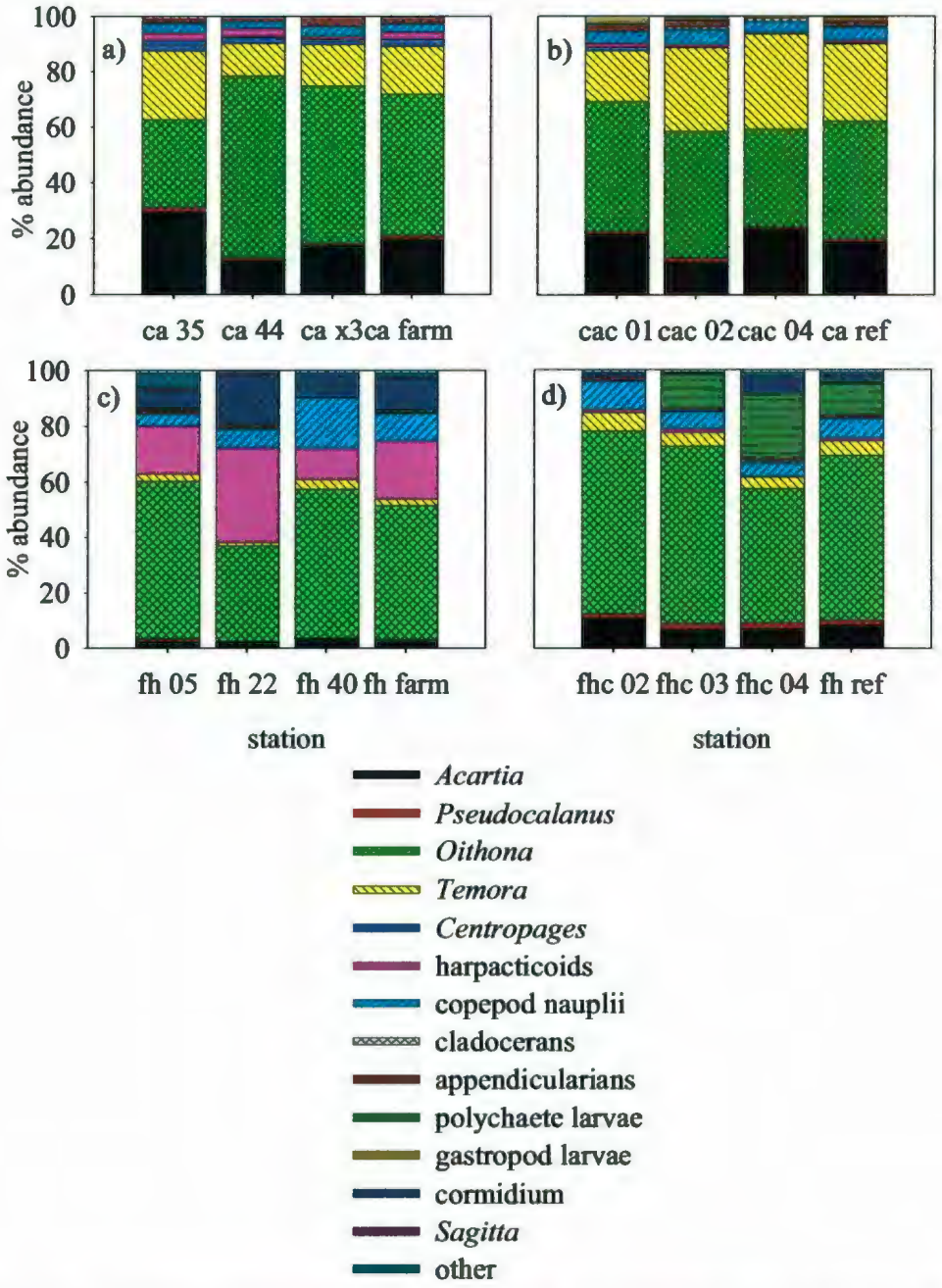

Figure 2.18: Zooplankton community composition in November 2001 for a) CA farm, b) CA ref, c) FH farm and d) FH ref.

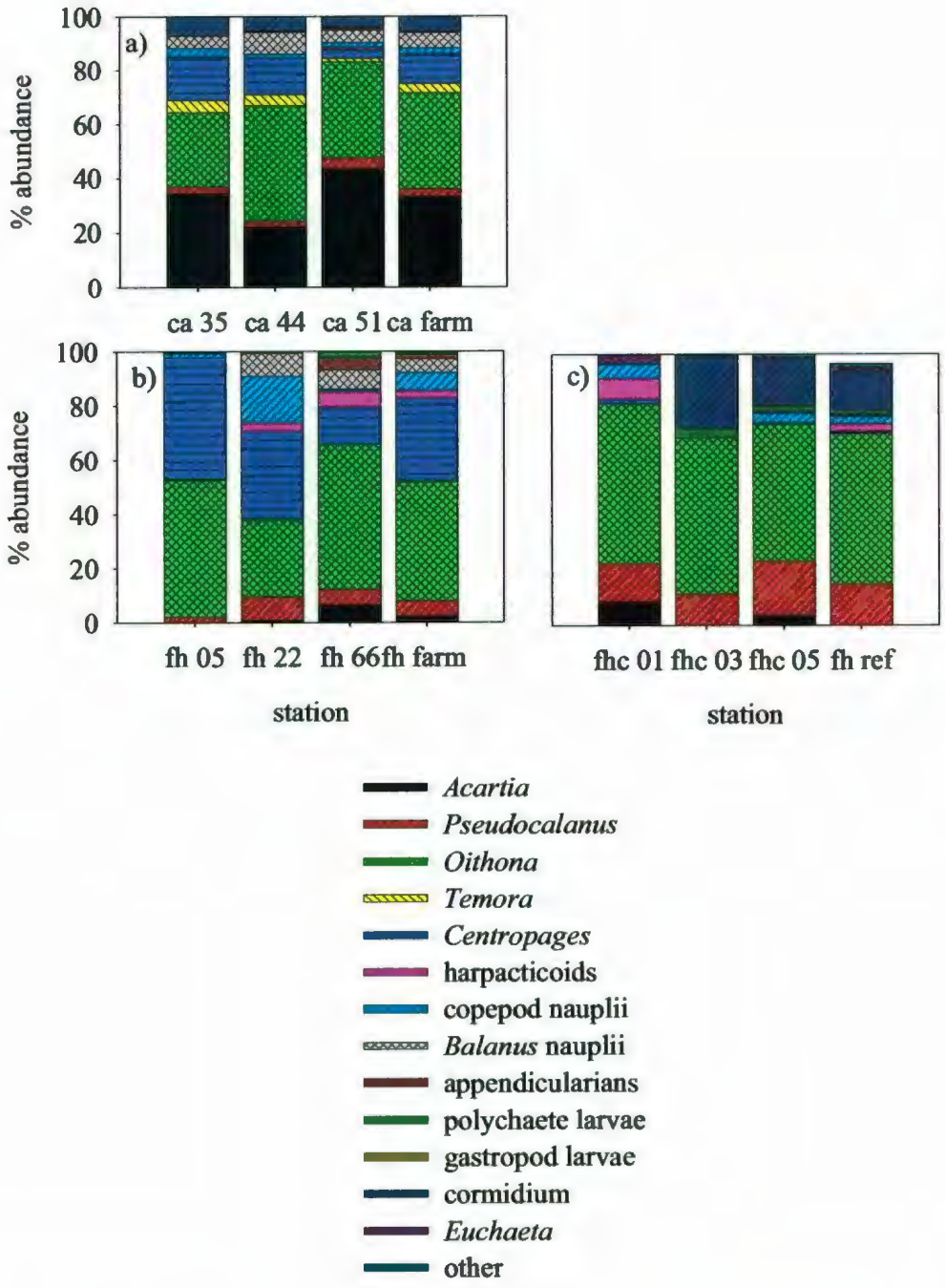

Figure 2.19 (a-c): Zooplankton community composition in March 2002 for a) CA farm, b) FH farm and c)FH ref.

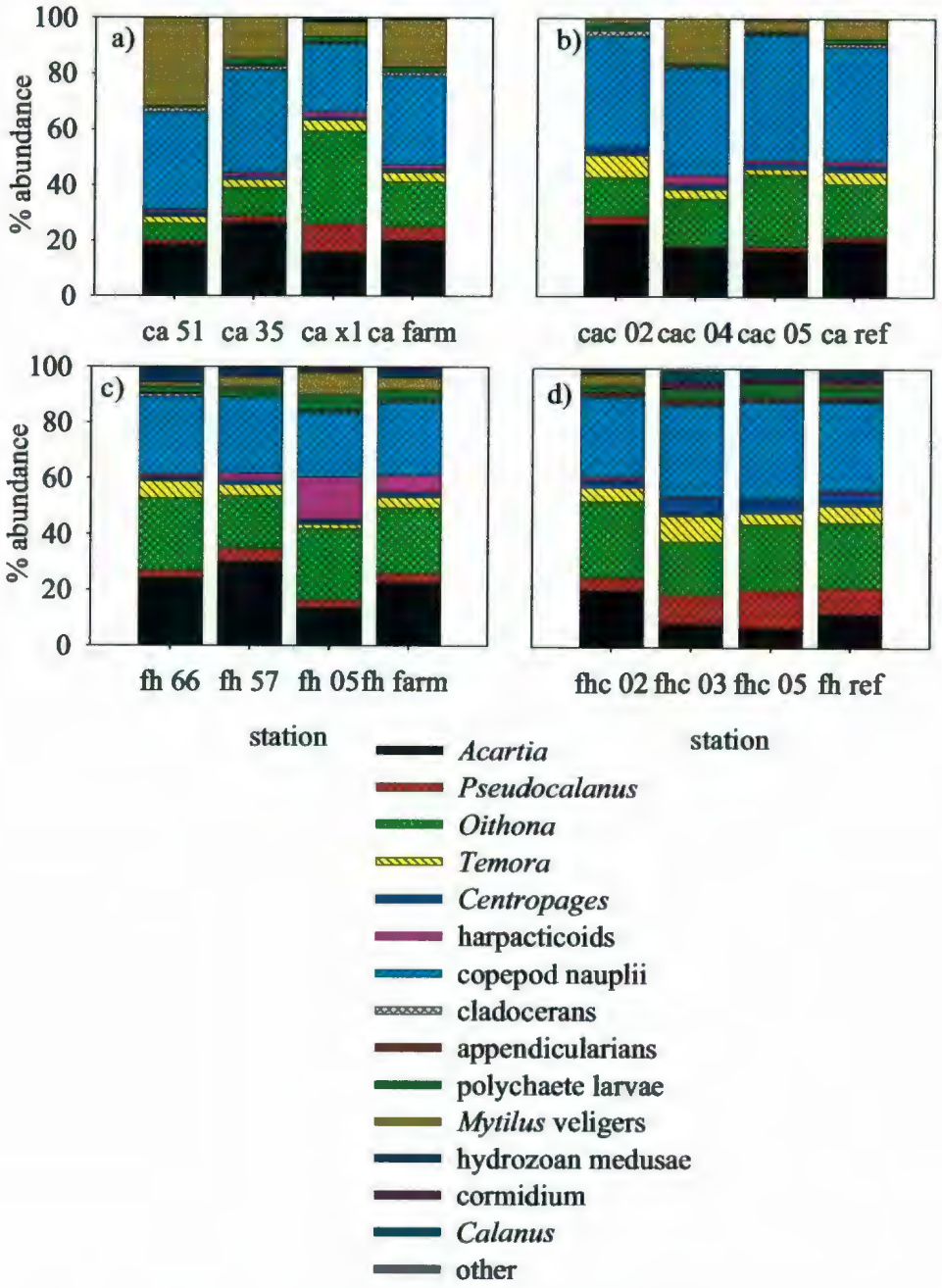

Figure 2.20: Zooplankton community compositions in July 2002 for a) CA farm, b) CA ref c) FH farm and d) FH ref.

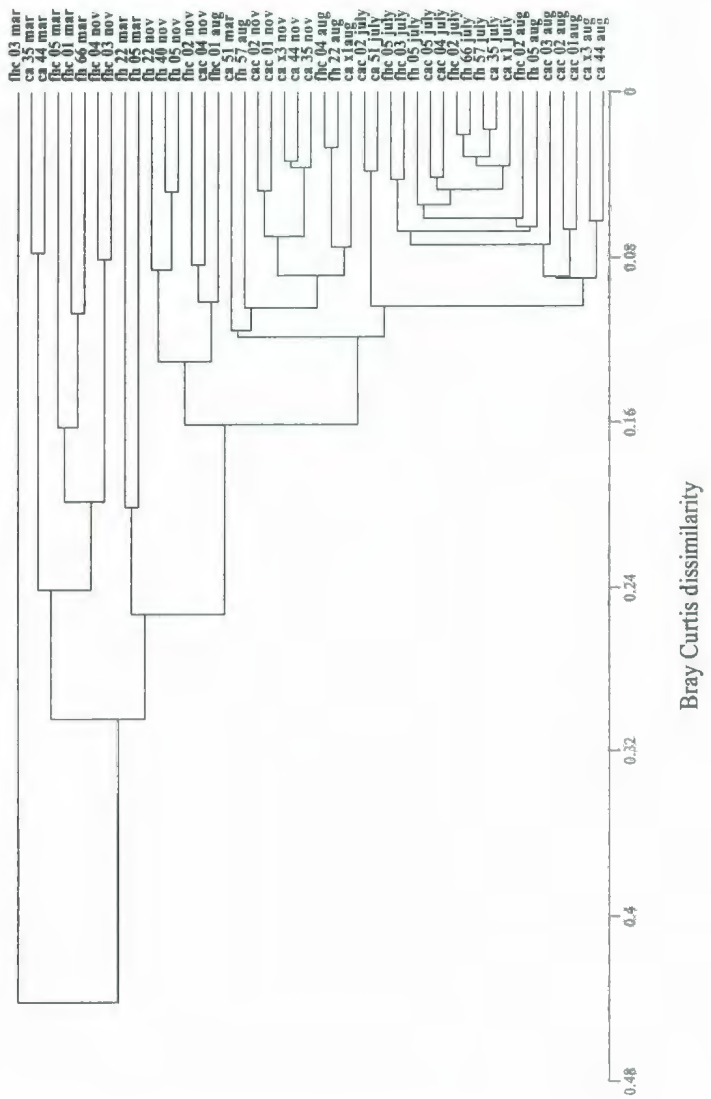

Figure 2.21: UPGMA clustering of the Bray-Curtis dissimilarity matrix of the community composition of all stations studied. CA refers to CA farm stations, CAC refers to CA reference stations, FH refers to FH farm stations, and FHC refers to FH ref stations. "aug" refers to August 2001, "nov" refers to November 2001, "mar" refers to March 2002 and "jul" refers to July 2002.

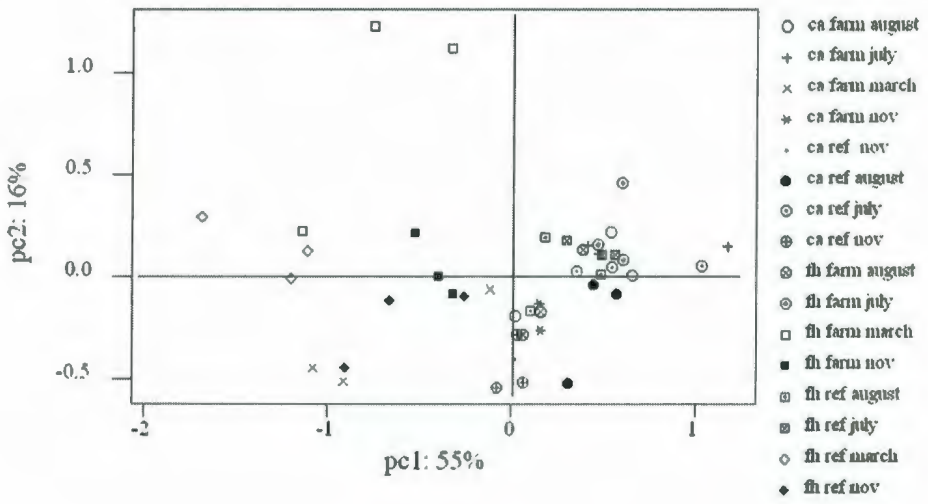

Figure 2.22: Factor loadings for the first two principle components of the community composition matrix

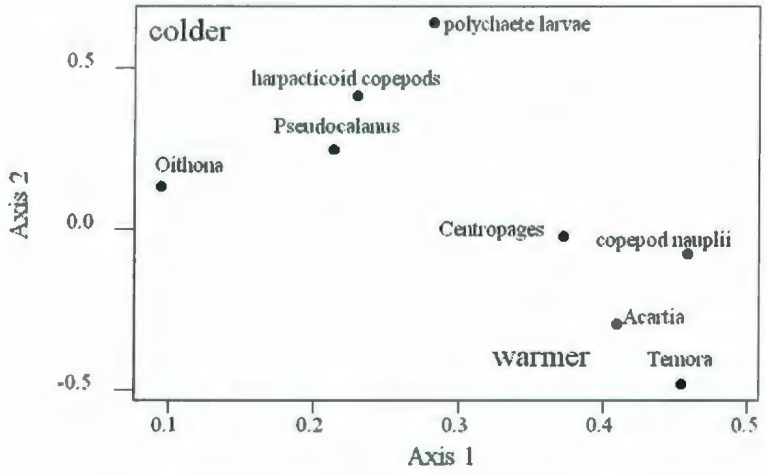

Figure 2.23: Case scores plot for the major taxa used in the priniciple components analysis

2.3.4 Seasonal, location and site effects on major taxa

General linear modeling was used to determine if there were seasonal differences in the abundance of major taxa or differences between farms and their references or between the FH and CA areas of Notre Dame Bay.

Except where indicated, abundance refers to volumetric abundance (i.e., #/m^3). Tests of significance were completed on the volumetric and areal data set and except where noted, the same results were obtained.

2.3.4.1 Seasonal effects on major species abundance

With the exception of harpacticoid copepods, abundance of the most common species showed clear seasonal differences (Table 2.4). *Pseudocalanus* sp. *Acartia* sp. *Temora* sp., *Centropages* spp. and copepod nauplii reached peak abundance in the warm sampling periods and lowest abundance in March 2002 (Table 2.5). *Oithona* sp. reached highest abundances in November 2001 and July 2002 and was least abundant in August (Table 2.5). For *Oithona* sp. the interaction term Season*Location was a significant predictor of abundance. For harpacticoid copepods the Season*Site and Season*Location interaction terms were significant. These indicate that location and/or site effects were seasonally different.

Table 2.4: Levels of significance of predictor variables in the general linear model of the volumetric abundance for the major taxa in the whole data set (four seasons studied).

Taxon	Season	Location	Site	Season* Location	Season* site	Location* Site
Acartia	**0.011**	**0.056**	0.422	0.417	0.763	0.792
Pseudocalanus	**0.001**	0.613	**0.024**	0.448	0.123	0.152
Oithona	**0.002**	0.165	0.108	**0.017**	0.126	0.721
Temora	**0.059**	**0.003**	**0.049**	0.210	0.666	0.234
Centropages	**0.005**	**0.087**	0.547	0.662	0.817	0.332
Harpacticoid copepods	0.967	**0.003**	**0.001**	**0.018**	**0.031**	0.385
Copepod nauplii	**0.002**	0.176	0.970	0.130	0.710	0.981
Polychaete larvae	**0.024**	**0.093**	**0.082**	0.135	0.145	0.861

Table 2.5: Mean (± standard deviation) of the volumetric abundance (N/m^3) of major taxa over the four study periods for all sites combined.

Taxa	August	November	March	July
Acartia sp.	1558 ± 986	617 ± 576	223 ± 530	2791± 3101
Pseudocalanus sp	532 ± 552	40 ± 19	155 ±208	459±303
Oithona sp.	2165 ± 964	2150 ± 975	1173 ±1794	2165±964
Centropages sp.	38 ± 59	38 ± 59	35±45	306± 284
Temora sp.	901± 695	698 ± 798	10 ± 20	580 ± 611
Harpacticoid copepods	273 ± 194	244 ± 353	835±1737	266±447
Copepod nauplii	1315 ± 999	252 ± 185	47 ± 82	4765 ± 5596
Polychaete larvae	105 ± 141	10±10	171 ± 421	277± 184

2.3.4.2 The effect of mussel farming on abundance of major taxa

Since the interaction term of Location*Site is not significant for any taxa in Table 2.9, the sites of both locations are grouped for comparison of farms and references. *Pseudocalanus* sp. (in August 2001), *Centropages* sp. (in November 2001) and harpacticoid copepods (August, November and March) were significantly more abundant at the farms than the reference sites. In addition, the abundance of *Pseudocalanus* sp as a proportion of the total abundance was higher ($F_{1, 11}$=8.50, p=0.015) at the farms (14±8 %) in August than at the reference sites (3.8 ± 2.0%).The areal abundance of *Acartia* sp. was higher at the farms (22732 ± 8937m^{-2}) than at the reference sites (11269± 7568 m^{-2}) in August ($F_{1, 11}$=5.75, p=0.037). The relative abundance of *Acartia* sp. was also higher ($F_{1, 11}$=12.86, p=0.005) at the farms (32± 7%) compared to the reference sites (16 ±7.4%).

Copepod nauplii (August 2001), *Temora* sp. (November 2001) and *Oithona* sp. (August 2001) were less abundant at the farms than at the reference sites. The relative abundances of copepod nauplii and *Temora* sp. were also lower at the reference sites.

Table 2.6: Mean ± SD of volumetric abundance (N/m^3) of taxa showing a significant difference between farms and references for each of the study periods. The upper line is the average farm value and the lower line is the average value for the references

Taxon	August	November	March
Acartia sp.	ns		
Pseudocalanus sp	820 ± 682 245 ± 88	ns	
Oithona sp.	651 ± 481 1120 ± 1083		ns
Centropages sp.		63.36 ± 73.65 12 ± 26	
Temora sp.	ns	447 ± 405 949 ± 1040	
Harpacticoid copepods	377± 229 170± 71	451± 412 37 ± 27	1248 ± 2052 10 ± 17
Copepod nauplii	633 ± 372 1997± 97	ns	ns
Polychaete larvae	ns		

2.3.4.3 Effects of position in Notre Dame Bay on abundance of major taxa

As indicated by the interaction between season and location in Table 2.9, season was a factor in the significance in the difference in abundance of *Oithona* sp. between FH and CA with a higher abundance at FH compared to CA in August ($F_{1, 11}$=30.91, p=0.001) and a higher areal abundance at FH (35619±9373 m^{-2}) compared to CA (20316±8772 m^{-2}) in July 2002 ($F_{1, 11}$= 8.53, p= 0.015). The abundance of *Acartia* and *Centropages* was higher at CA compared to FH in November, 2001. Abundance of *Temora* sp. was higher at CA compared to FH in March 2002.The abundance of harpacticoid copepods was higher at FH in August ($F_{1,11}$=0.19, p=0.09) and November, 2001 and March 2001, the seasonal dependence being indicated by the significant interaction term in Table 2.4.

Table 2.7: Mean ± SD of volumetric abundance (N/m^3) of taxa showing a significant difference between at CA (upper line) and FH (lower line) during each of the study periods. CA and FH include the farms and reference sites in each location There were no significant differences in July 2002.

	August	November	March
Acartia sp.	ns	1076 ± 455 158 ± 133	
Pseudocalanus sp		51 ± 17 28 ± 15	ns
Oithona sp.	238 ±111 1553 ±720	ns	
Centropages sp.	ns	75.50 ± 65.3 0± 0	
Temora sp.		1285 ± 752 111 ± 848	30 ± 25 0 ± 0
Harpacticoid copepods	ns	83.2 ± 55.4 405 ± 456	8 ± 13 1249 ± 2052
Copepod nauplii		ns	ns
Polychaete larvae			

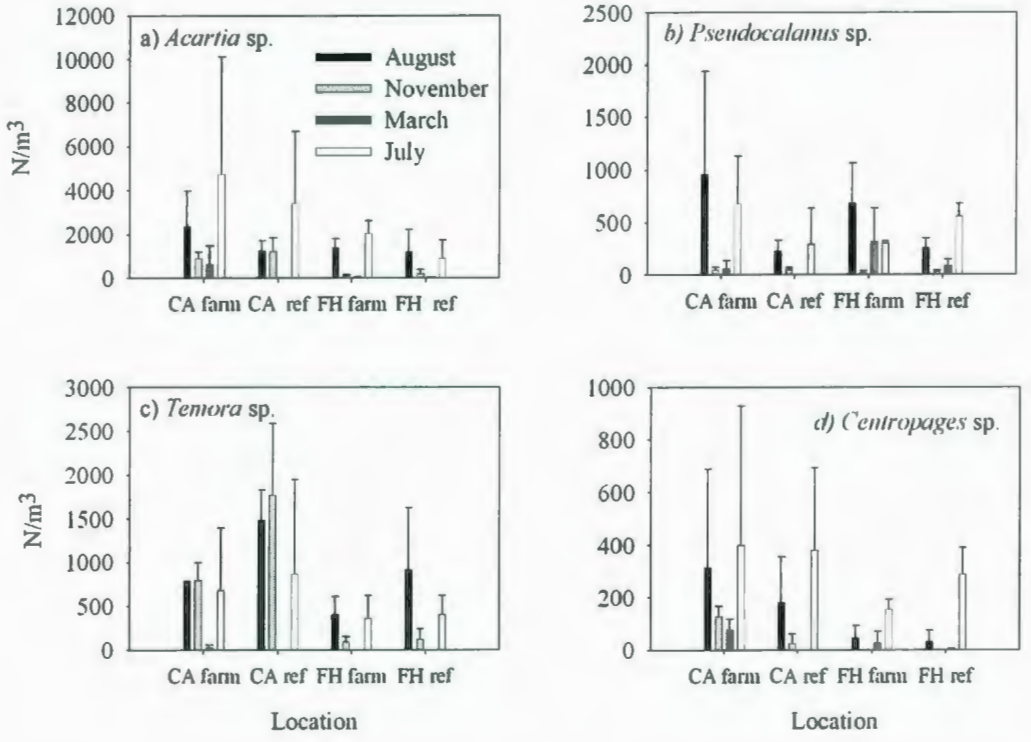

Figure 2.24: Volumetric abundances (N/m^3) of major calanoid copepods in the four study sites in all four study periods. The error bars represent the standard deviation from the mean of three stations per location.

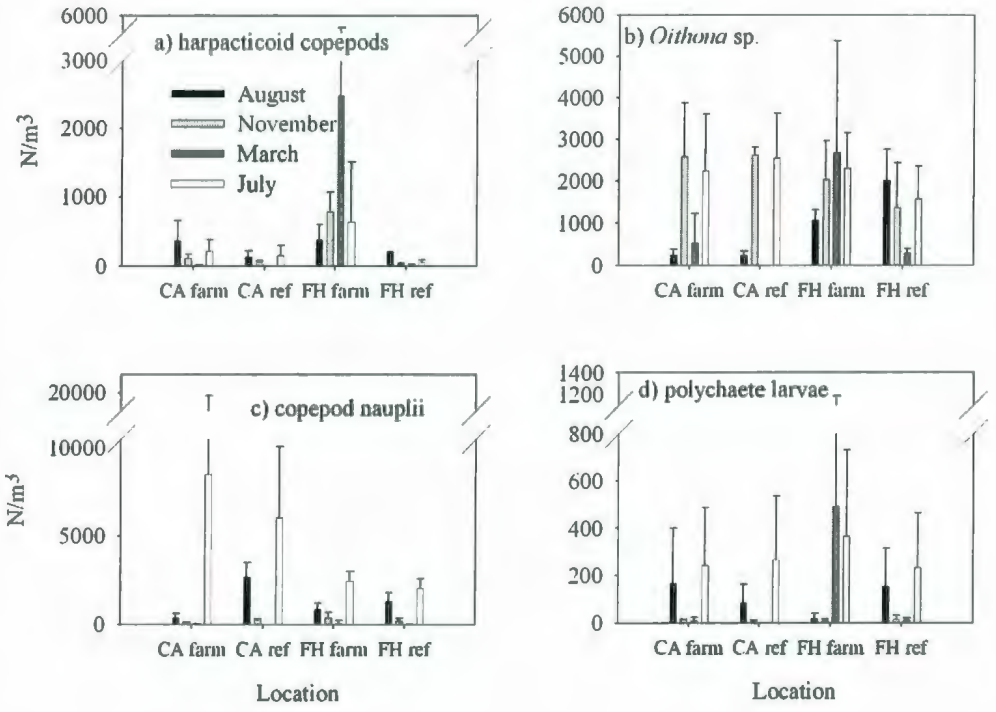

Figure 2.25: Volumetric abundance of major non-calanoid copepod zooplankton in the four study periods. The error bars represent the mean of three stations per location.

2.3.5 Small animal abundance

The abundance of small animals varied significantly with season (Table 2.8) with the highest values in the warmest seasons of July 2002 (12640±11861m^{-3}) and August 2001 (6092±2238 m^{-3}) followed by November 2001 (4230±1738 m^{-3}) and March 2002 (2582±3391 m^{-3}) (Figure 2.26). It did not vary between sites in Notre Dame Bay or between farms and reference sites. While distance from the head of the farm was a significant predictor of the abundance of small animals, it explained only 5.2% of the total variation.

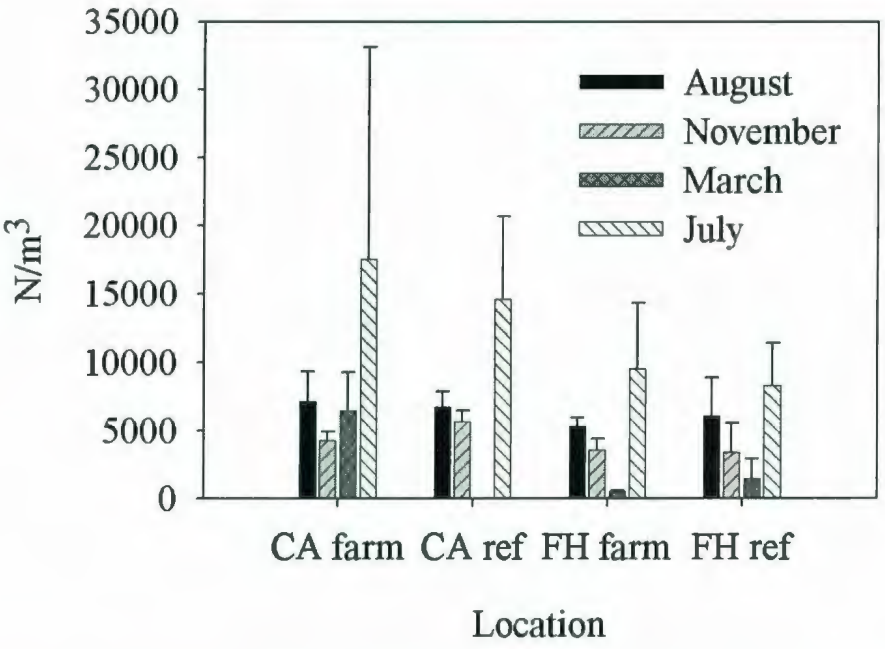

Figure 2.26: Volumetric abundance of small animals for each of the periods studied. The bars represent the mean of all stations sampled and the error bars represent the standard deviation from the mean.

Table 2.8: General linear model ANOVA table of small animal abundance (volumetric whole data set)

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Distance	1	200274484	195928179	195928179	3.74	**0.058**
Season	1	391555715	398903053	398903053	7.62	**0.008**
Location	1	196671610	7701646	7701646	0.15	0.703
Site	1	46349966	562966	562966	0.01	0.918
Location*Season	1	96747837	95026303	95026303	1.81	0.183
Site*Season	1	17423498	17229960	17229960	0.33	0.568
Location*Site	1	77868	127824	127824	0.00	0.961
Location*Site*Season	1	68654	68654	68654	0.00	0.971
Error	56	2932000036	2932000036	52357143		
Total	64	3881169667				

2.3.6 Large animal abundance

The abundance of large animals did not vary significantly with season alone and did not differ between farms and their reference sites (Table 2.9) There was a significant interaction between season and location (Table 2.9) Large animals were more abundant at CA (407±241/m^3) than at FH (202±225/m^3) in general and in November (with 357±113/m^3 at CA compared to 92±60 /m^3 at FH) and August (603±231/ m^3 at CA compared to 140±61/m^3 at FH)

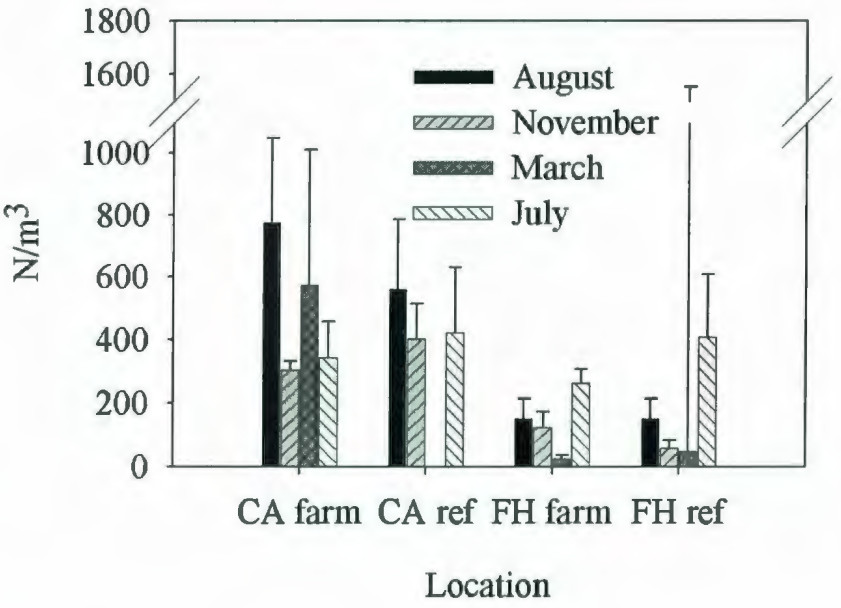

Figure 2.27: Abundance (N/m^3) of large animals for each of the periods studied. The bars represent the mean of all stations sampled and the error bars represent the standard deviation .

Table 2.9: General linear model of large animal abundance (volumetric whole data set) with distance and season as covariates

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Distance	1	4323	30224	30224	0.62	0.436
Season	1	589	1130	1130	0.02	0.880
Location	1	686716	962167	962167	19.61	**0.000**
Site	1	1637	41787	41787	0.85	0.360
Location*Season	1	477661	457171	457171	9.32	**0.003**
Location *Season	1	44921	47264	47264	0.96	0.331
Location*Site	1	93030	174	174	0.00	0.953
Location*Site*Season	1	26430	26430	26430	0.54	0.466
Error	56	2747340	2747340	49060		
Total	64	4082648				

Table 2.10: Seasonal summary of the significance of location in Notre Dame Bay and site to large animal abundance

Season	Explanatory variable	F	p
August, 2001	**Location**	14.01	**0.002**
	Site	0.45	0.513
November 2001	**Location**	6.09	**0.028**
	Site	0.08	0.787
March 2002	Location	3.45	0.105
	Site	3.11	0.121
July 2001	Location	2.21	0.155
	Site	0.64	0.436

2.3.7 Power analysis of abundance

Table 2.11 shows the minimum detectable difference based on the whole data set of the large and small animal abundances for location and site as explanatory variables. These differences indicate that smaller differences between farms and references could be detected than differences between locations within Notre Dame Bay.

Table 2.11: Minimum detectable percentage difference for the whole abundance data set, based on $\alpha = 0.05$. The asterisk indicates that a significant difference was detected.

Response variable	Predictor	
	Location	Site
N_{small}/m^3	74	89
N_{large}/m^3	*	56

2.3.8 Biomass

Considering the whole data set (Figure 2.28, Table 3.18) the farms (65.6±73.7mg/m^3) had a larger overall mean biomass than the reference sites (38.8±48.4 mg/m^3). In March, location in Notre Dame Bay was a significant predictor ($F_{1,8}$=26.77, p=0.002) of biomass with CA having a higher biomass than FH. In July the farms had a higher biomass than their reference sites ($F_{1,19}$=3.06, p=0.099).

Table 2.12: ANOVA table for the GLM of volumetric biomass for all seasons studied

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Location	1	16688	9675	9675	2.68	0.108
Site	1	11041	14038	14038	3.89	**0.054**
Season	3	21141	22021	340	2.03	0.121
Location*Site	1	5925	5925	5925	1.64	0.206
Error	52	187848	187848	3612		
Total	58	242643				

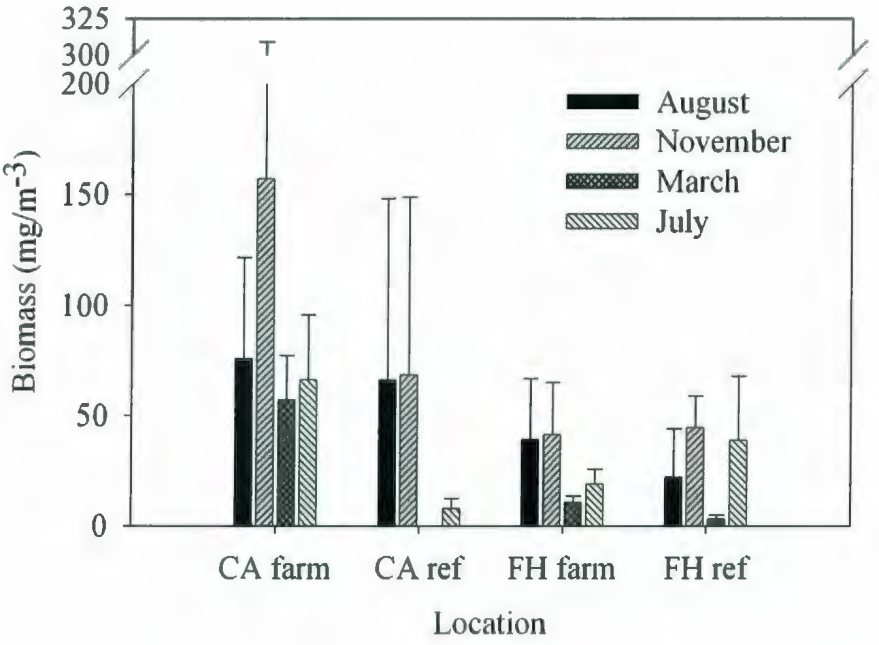

Figure 2.28: Average biomass (mg lyophilized dry mass per cubic m) at each of the study locations for each of the periods studied. The errors bars represent the standard deviation of the mean of three to five stations.

2.4 Discussion

2.4.1 Limitations of comparisons

Adjacent embayments can have, without anthropogenic perturbation, different patterns of abundance and dominance of resident species even if many of the species are the same (Kimmerer and McKinnon, 1985). Comparisons of locations and sites in this study are therefore made with the knowledge that the sites studied do not all have the same shape and that the observations at each site and location are separated in time. The presence of the sills at the farms and not at the reference sites may affect community composition as well (Gagnon and Lacroix, 1983). The narrowness of the mouth of Charles Arm may trap living and non-living particles, which may magnify the effect of grazing by mussels.

Short term temporal variability might play a role in some of the differences observed. This is an especially important caution with respect to comparisons between locations in Notre Dame Bay as these are sampled with the longest time interval between them (up to one week). It is less problematic with respect to the comparisons between different sites within locations as these observations are separated by one day only and the profiles of salinity, temperature and density of the sites are consistently similar to each other.

Comparisons of physical profiles between locations in Notre Dame Bay indicate differences in the degree of water column stratification. While there may be a temporal component to this difference, the stronger stratification at FH has been consistently

observed at all sample periods. Nevertheless, in instances where location is a significant predictor of a variable, it is more accurate to state that the variable at CA is different from that of FH about one week later and where site is a significant predictor, the variable at the farm is different from that of the reference site sampled one day later. Given that expense and logistic concerns made it impossible to sample all stations for all sites and locations on the same day, the sampling plan used was the best effort to account for variations based on time of day and tidal stage with samples taken at approximately the same time of day and tidal stage. We are aware that the "before-after-treatment-control" approach would be most desirable in this type of study (Green, 1979) but this was not possible as both farms were in place before our study was funded.

2.4.2 The effect of mussel farming on Notre Dame Bay plankton communities

The presence of a mussel farm had no significant effect on the abundance of small and large animals. However, species-specific abundance was affected by the presence of the farms. *Pseudocalanus* sp., *Centropages* sp., harpacticoid copepods and *Acartia* sp (areal and relative abundance of the latter) were more abundant at the farms that at the reference sites. *Temora* sp., *Oithona* sp. and copepod nauplii were less abundant at the farms than at their reference sites. The effects on individual taxa were observed during the sampling period in which they were most abundant.

The age and extent of coverage of these sites may be a factor in their pronounced effect on the abundance of certain zooplankton. Grant et al (1998) found that zooplankton may take a significant proportion of the food that would otherwise be available to mussels in younger, smaller mussel farms, while in older sites, mussels will consume more food than do the resident zooplankton.

The differences in impact among the various groups of zooplankton may be predation driven, arising from differences in vulnerability to mussel grazing, or resource driven, arising from differences in the level of competition with mussels for food or in the ability to utilize food particles present in the farms compared to the reference sites. Effects may be more obvious for taxa such as *Acartia* which has been shown to have position keeping capabilities which allows them to remain in favorable environments and to form resident populations (Bucklin, 2000). In the case of harpacticoid copepods such as *Microstella* and *Tisbe* sp. which are benthic and tend to favor complex substrates (Jenkins, Walker-Smith and Hamer, 2002), the ropes and gear of a mussel farm and the associated macroalgal epiphytes provide greater habitat complexity.

Acartia and *Centropages* may be able to take advantage of the farms' food environment due to their nutritional flexibility (Davis, 1987; Kiorbe and Saiz, 1995; Kiorbe, Saiz, and Viitasalo, 1996). Mussel farms often have higher levels of detritus. This may make the farms nutritionally superior environments as detritus for the above species as detritus has

been shown to provide additional fatty acids and proteins which may aid in growth (Berggreen et al, 1988; Kleppel, 1992; Roman, 1984). *Centropages* may benefit from the mixed autotrophic population at the farm (Penney et al, 2001) as its growth rate is higher when large diatoms and small ciliates and flagellates are all included in their diet (Davis, 1987). The farm may also be richer in those autotrophic species that are able to utilize the ammonia produced by the mussels after the main diatom bloom has exhausted nitrate nitrogen (Mengesha et al, 1998).

The negative effect of the mussel farms on copepod nauplii, *Temora* and *Oithona* likely reflects an increased vulnerability to mussel ingestion. Copepod nauplii are in the size range easily ingested by mussels (Green et al., 2003) and bactivory usually prevents food limitation (Roff, 1995). The negative impact on adult and juvenile *Temora* sp. in November may reflect an increased negative impact on their nauplii in the summer. *Temora* nauplii may be less able to escape the flow field of mussels than are those of other zooplankton nauplii such as *Acartia* sp (Green et al., 2003).

The lower abundance of *Oithona* sp at the farm is not likely due to lack of suitable food. Autotrophic food particles preferred by *Oithona* sp. (Nakamura et al, 1997) are present at the farms and the increased levels of mussel faecal material at the farms might otherwise be advantageous for species exhibiting coprophagy such as *Oithona* (Gonzalez and Smetacek, 1994). Therefore competition with mussels for food resources is a more

probable factor in their lower abundance at the farms compared to their reference sites. As well, recruitment levels may be decreased when female *Oithona* carrying eggs are ingested by mussels.

One must interpret cautiously the higher total biomass at the farms compared to their reference sites since the biomass estimates take all particles above 110 μm into account including detritus, faeces and large diatoms. This was qualitatively a more significant concern in March 2002, where samples were dtrongly contaminated by mussel faecal pellets. As the total abundance is not affected by the presence of the farm, a higher biomass at the farms may be due to a higher mean individual biomass of *Acartia* sp., *Pseudocalanus* sp., *Centropages* or harpacticoid copepods (which are more abundant at the farms than at the reference sites) or higher biomass of all taxa present at the farm. Species specific biomass estimations are necessary to further explore the nature of the impact on biomass.

2.4.3 Impacts of zooplankton community changes

The observed differences between farms and their refereneces may affect the export of organic matter to the benthos and the activity of the microbial and metazoan food webs. As the consumption of faecal and detrital material by *Oithona* spp. normally prevents some organic matter from reaching the bottom (Beaumont et al, 2001; Gonzalez and

Smetacek, 1994; Gonzalez et al, 1994; Nielsen and Sabatini, 1996) the decreased abundance of *Oithona* sp. at the farms compared to their refernces in March and

November may contribute to an increased export of organic matter to the benthos at the farms. As nauplii feed on smaller particles (such as bacteria) than do larger adult copepods, reduction of their abundance by mussels divert some of the microbial food web energy normally transferred to other metazoans at higher trophic levels through the nauplii to mussels (Roff et al, 1995). The decrease in the abundance of nauplii at the farms may also have consequences for the recruitment of those copepod taxa whose nauplii are most vulnerable to predation.

Some of the other taxa affected by mussel farming are important components of the diet of juvenile fish in nearshore habitats in Newfoundland. Grant and Brown (1998) found the gut contents if age-0 cod in this area were composed of up to 30 to 60% *Temora* sp. in October and up to almost 80% in November. Whether juvenile cod in Notre Dame Bay may be negatively affected by a decrease in the abundance of *Temora* sp is uncertain. Preference for prey may be also be dependent on nutritional value and relative size (Munk, 1997) and prey switching might occur.

2.4.4 Differences in community composition between areas of Notre Dame Bay

The differences in community composition between the Fortune Harbour area and the Charles Arm area may be related to the physical differences between the two sites. The increased abundance of *Oithona* sp. in FH, especially in August, may be related to the increased stratification in FH compared to CA. Species shifts from *Acartia* sp. to *Oithona* sp. have occurred in mesocosm experiments with the introduction of a pycnocline (Sullivan, 1995). The FH area also had qualitatively more detritus than did CA which may confer an advantage to *Oithona* in FH given its feeding habits as discussed earlier.

The increased abundance of *Acartia* sp., *Pseudocalanus* sp., *Centropages* sp. and *Temora* sp. at CA compared to FH in the fall may indicate higher productivity at that time in the more inshore, enclosed parts of NDB as these species tend to reach peak abundance in areas of highest productivity (Gaard, 1999). Salinity differences may also play a role as FH is slightly more saline than CA and these species have been found in higher abundance in areas of lower salinity (Gaard, 1999).

2.4.5 Zooplankton community characteristics in Notre Dame Bay: comparisons with other areas

The dominance of only a few species and of smaller size fractions in coastal Notre Dame Bay is consistent with other coastal areas exhibiting a wide range of physical characteristics. *Acartia* sp. and *Temora* sp. are characteristic of nearshore waters in the Barents Sea (Musaeva and Gagarin, 2000), the Faroe Shelf (Gaard, 1999), the Mediterranean Sea (Calbet et al, 2001;Siokou-Frangou et al, 1998) and the Irish Sea (Gowen et al, 1999). In the Mediterranean, for example, ten copepod species, including *Acartia*, *Temora* and *Centropages*, may account for up to 52% of the total zooplankton with only minor differences in rank order within or among years (Mazzocchi and D'Alcala, 1999). In the North Sea, the combination of *Pseudocalanus* and *Temora* sometimes accounted for 95% of the population (M'harzi et al, 1998). Many of these species are omnivorous (*Temora*, *Acartia* and *Centropages*) and their nutritional flexibility may be a strategy that enables them to thrive in the variable coastal environment (Ohman and Runge, 1994).

The importance of *Oithona* sp. in Notre Dame Bay, in particular, is a common feature of shallow coastal environments, especially when calanoid populations are low or when eggs of calanoids are lost to the benthos (Nelsen and Sabatini ,1996). In shallow regions of the North Sea *Oithona* sp. can amount to 50% of the total copepod biomass, 70% of the production (Nielsen and Sabatini, 1996) and up to 75% of the total abundance - the

bulk of the < 500-μm fraction (Arashkevich et al 2002). According to Paffenhoffer (1993) the lack of specialization compared to calanoids may allow species of Oithonidae to withstand a wider range of environmental conditions and to utilize small phytoplankton which are inefficiently grazed by larger calanoids. The predominance of *Oithona* during some seasons may indicate a periods of increased activity of the microbial food web (Gonzalez and Smetacek, 1994; Gonzalez et al., 1994). Peak abundances of *Oithona* sp. occur around the time of the fall and spring blooms in Notre Dame Bay when, especially at the mussel farms, the release of faecal pellets may stimulate the microbial food web. At the reference sites, they may be utilizing the faeces of other zooplankton.

In general, total abundance of zooplankton at these sites was lower than in comparable areas such as Norwegian fjords where the abundance of *Oithona similis*, *Acartia* sp. and *Pseudocalanus* sp. can each reach >50000 individuals m^{-3} and higher than in the polluted areas of the Black Sea where total zooplankton reaches a high 12000 m^{-3} in June (Falkenhaug et al, 1997; Mutlu, 2001). The abundance of *Acartia* in NDB was very much higher than values recorded by Davis (1982) for Conception Bay but lower than that of the Lower St. Lawrence Estuary where summer abundances sometimes reached up to 100000 m^{-3} (Archambault et al, 1998). *Temora* sp. were less abundant and *Centropages* more abundant than in Conception Bay (Davis, 1982).

The zooplankton biomass observed in this study was lower than that of some other similar coastal areas. Nearby on the Northeast shelf of Newfoundland, Dalley and Anderson (1998) found dry weights of animals <1mm of ~3mg DM/m^2 and ~2.5-3 mg DM m^{-2} for animals 1-2 mm in the summer of 1998, (though they do state that it was higher than for most other years). Summer zooplankton biomass in the Hudson Bay region of Canada was 1.6 g m^{-2} in summer (Harvey, Therriault, and Simard, 2001). These values are much higher than the values observed at any of our study sites in August 2001 (CA farm 0.64 g m^{-2}, CA ref 1.0 g m^{-2}, FH farm 0.68 g/m^2, FH ref 0.2 g m^{-2}). Previous work in Charles Arm (Penney et al, 2001) , however, has shown that despite some years of anomalously low levels, in most years maximum *total* particulate matter is higher than other, more open water coastal areas of Newfoundland (Navarro and Thompson, 1995).

Most species exhibited high abundance in the warm months of July and August in this study, indicating that most of their production probably occurs after the spring bloom. High summer abundance for some taxa is common in many coastal environments including Conception Bay, Newfoundland (Davis, 1982). The pattern of two periods of high abundance of *Oithona* sp. in early spring and late fall was also similar to that of Conception Bay although peak abundances there were lower than in the present study (Davis, 1982). Lack of seasonality in the abundance of larger animals as a group (those

taken by a coarser net) has been shown in other areas such as the Norwegian and Barents Seas (Tande et al, 2001).

Multivariate analysis separated warm water Notre Dame Bay communities dominated by *Acartia* sp. *Temora* sp. and *Centropages* sp. from cold water communities including *Pseudocalanus* and *Oithona* sp. *Pseudocalanus* is also a dominant winter species on the Faroe Shelf where Gaard (1999) speculates, it may benefit from decreased competition with other copepods as the diatom biomass gradually decreases. In contrast to Notre Dame Bay, in the warmer waters of the Mediterranean, *Acartia* sp and *Centropages* are associated with colder seasons (Siokou-Frangou et al, 1998). *Temora* is associated with warmer seasons there as in Notre Dame Bay (Siokou-Frangou et al, 1998). While the grouping of *Centropages* and *Temora longicornis* in the present study is similar to that of the temperate English channel, *Acartia* is associated with assemblages of cyclopoid and harpacticoid copepods there (Mouny and Jauvin, 2002).

2.4.6 Predators other than mussels

In well mixed coastal environments biological interactions such as predation and avoidance of predators may be more important in structuring the planktonic community than are the effects of salinity, and density driven water motion (Wiafe and Frid, 1996). Medusae are periodically very abundant in NDB and may be exerting a strong control of

the plankton populations there as they do in other areas. In Danish fjords, for example, jellyfish blooms are often concurrent with the disappearance of copepods (Nielson, Pederson, and Riisgard, 1997). The ability of medusae to process water rivals that of mussels, with populations of *Aurelia* sp. being able to clear the entire water column 3.5 times per day in summer in shallow coves (Olesen, 1995).

The impact of blooms of medusae such as *Aurelia* sp. can include changes in zooplankton community composition. *Oithona similis* and *Pseudocalanus sp.* were less abundant in a bloom year of *A. aurita* in the western Baltic while *Centropages humatus* or *Acartia* sp. were not significantly affected (Schneider and Behrends, 1998). In the Black Sea, *Acartia clausii* and *Pseudocalanus* were major constituents of the gut contents of *Aurelia* sp (31 and 26% respectively; Mutlu, 2001). Gut content analysis of *Aurelia aurita* by Graham and Kroutil (2001) also indicated that small copepods tend to be consumed by only very large medusae (larger than ~13 cm in diameter in the Gulf of Mexico and ~8cm in Narrangaset Bay). Thus *Aurelia* sp. may be a controlling predatory force on larger copepods and less on smaller species such as *Oithona* sp.

2.4.7 Recommendations

This is the first study of its kind except for an inconclusive study on a Mediterranean lagoon (Lam-Hoi and Rougier, 2001) and as such recommendations for future studies are

especially relevant. Because this study suggests negative effects of mussel farming on copepod nauplii and *Oithona* sp., more efficient measurement of the abundance of smaller zooplankton is needed. In particular, nets with smaller mesh size (perhaps 64 μm) in conjunction with pump sampling would improve the probability of detecting differences in these smaller organisms as well as the sampling of rarer taxa. Use of smaller mesh in nets has been recently identified as necessary to reveal the true importance of smaller size fractions which may be underrepresented by the coarser nets usually used (Gallienne and Robin, 2001). Because the community composition suggests seasonal cycles in zooplankton production it is important that monitoring be carried out more often than quarterly. In addition, if time and resources permit, a sampling program is needed to assess short term variability in the communities (over several days and several tidal cycles for example).

Given the possible impact of large gelatinous zooplankton on community composition and their potentially important role in nitrogen cycling, a study of their seasonal cycles of biomass and abundance would be important in determining controls on zooplankton populations and carrying capacity of the farms.

2.5 References

Arashkevich, E., Wassmann, P. et al. (2002) Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. Journal of Marine Systems 38: 125-145.

Archambault, P., Roff, J., Bourget, E., Bang, B., and Ingram, G. (1998) Nearshore abundance of zooplankton in relation to coastal topographic heterogeneity and the mechanisms involved. Journal of Plankton Research 20: 671-690.

Asmus, R. and Asmus, H. (1991). Mussel beds: limiting or promoting phytoplankton? Journal of Experimental Marine Biology and Ecology 148, 215-232.

Beaumont, K., Plummer, A., Hosie, G., and Ritz, D. (2001) Production and fate of faecal pellets during summer in an East Antarctic fjord.Hydrobiologia 453/454: 55-65.

Bucklin, A., Kaartvedt, S., Guarnier, M., and Goswami, U. (2000) Population genetics of drifting (*Calanus* spp.) and resident (*Acartia clausii*) plankton in Norwegian fjords. Journal of Plankton Research 22(7): 1237-1251.

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., and Duarte, C. (2001) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. Journal of Plankton Research 23(3): 319-331.

Clemens, T., Couturier, C., Parsons, G., and Dabinett, P. (2000) *Environmental characteristics of Newfoundland shellfish farms for 1995-1999: ACERA mussel project #1* St. John's, NL: Memorial University of Newfoundland.

Cranford, P. and Hill, P. (1999) Seasonal variation in food utilization by the suspension feeding bivalve molluscs *Mytilus edulis* and *Placopectan magellanicus*. Marine Ecology Progress Series 190, 223-239.

Crocker, K. (1998) *Tracking and growth of larvae of the giant scallop, Placopectan magellanicus (Gmelin, 1791) on a scallop farm in Notre Dame Bay, Newfoundland.* Master of Science Aquaculture, Memorial University of Newfoundland.

Dalley, E., Anderson, J. and Davis, D. (1999) Plankton and nekton of the northeast Newfoundland shelf and Grand Banks in 1998. Canadian Stock Assessment Secretariat Research Document 99/142.

Davenport, J., Smith, R., and Packer, M. (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Marine Ecology Progress Series 198, 131-137.

Davis, C. (1982) A preliminary quantitative study of the zooplankton from Conception Bay, Insular Newfoundland, Canada. Int.Revue.ges.Hydrobiol. 67(5): 713-747.

Davis, C. (1987) Predatory control of copepod seasonal cycles on Georges Bank. Marine Biology. 82: 31-40.

Falkenhaug, T., Tande, K. and Timonin, A. (1997) Spatio-temporal patterns in the copepod community in Malangen, northern Norway. Journal of Plankton Research 19: 449-468.

Gallienne, C. and Robins, D. (2001) Is *Oithona* the most important copepod in the world's oceans? Journal of Plankton Research 23(12): 1421-1433.

Gaard, E. (1999) The zooplankton community structure in relation to its biological and physical environment on the Faroe Shelf, 1989-1997. Journal of Plankton Research 21(6): 1133-1152.

Gagnon, M. and Lacroix, G. (1983) The transport and retention of zooplankton in relation to a sill in a tidal estuary. Journal of Plankton Research 5(2): 289-303.

Gasol, J., Giorgio, P. and Duarte, C. (1997) Biomass distribution in marine planktonic communities. Limnology and Oceanography 42(6): 1353-1363.

Grant, S. and Brown, J. (1998) Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. Can J Fish Aquat Sci 55: 1307-1316.

Grant, J., Stenton-Dozey, J., Monteiro, P., Pitcher, G., and Heasman, K. (1998) Shellfish culture in the Benguela system: a carbon budget of Saldanha Bay for raft culture of *Mytilus galloprovincialis*. Journal of Shellfish Research 17(1): 41-49.

Green, J. (1979) Sampling design and statistical methods for environmental biologist. New York: Wiley Interscience.

Green, S., Visser, A., Titelman, J., and Kiorbe, T. (2003) Escape responses of copepod nauplii in the flow field of the blue mussel, *Mytilus edulis*. Marine Biology 142(4): 727-733.

Gonzalez, H. and Smetacek, V. (1994) The possible role of the cyclopoid copepod *Oithona* in retarding the vertical flux of zooplankton faecal material. Marine Ecology Progress Series 113: 233-246.

Gonzalez, H., Kurbjewit, F., Bathmann, U. (1994) Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January-February 1991. Polar Biology 14: 331-342.

Gowen, R., McCullough, G., Kleppel, G., Houchin, L., and Elliot, P. (1999) Are copepods important grazers of the spring phytoplankton bloom in the western Irish sea. Journal of Plankton Research 21(3): 465-483.

Graham, W. and Kroutil, R. (2001) Size-based prey slectivity and dietary shifts in the jellyfish, *Aurelia aurita*. Journal of Plankton Research 23(1), 67-74.

Harvey, M., Therriault, J.-C., and Simard, N. (2001) Hydrodynamic control of late summer species composition and abundance of zooplankton in Hudson Bay and Hudon Strait (Canada). Journal of Plankton Research 23(5):481-496.

Horsted, S., Nielson, T., Pock-Steen, J., and Koefoed Bjoremsen, P. (1988) Regulation of zooplankton by suspension-feeding bivalves and fish in estuarine enclosures.Marine Ecology Progres Series 48(3): 217-224.

Jenkins, G., Walker-Smith, G., and Hamer, P. (2002) Elements of habitat complexity that influences harpacticoid copepods associated with seagrass beds in a temperate bay. Oecologia 131, 598-605.

Kaiser, M., Laing, I., Utting, S., and Burnell, G. (1998). Environmental impacts of bivalve mariculture. Journal of Shellfish Research 17(1): 59-66.

Kiorbe, T. and Saiz, E. (1995) Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. Marine Ecology Progress Series 122: 135-145.

Kiorbe, T. Saiz, E. and Viitasalo, M. (1996) Prey switching behavior in the planktonic copepod *Acartia tonsa*. Marine Ecology Progress Series 143: 65-75.

Kleppel, G. (1992) Environmental regulation of feeding and egg production by *Acartia tonsa* off Southern California . Marine Biology 112(57): 65.

Lam-Hoi, T. and Rougier, C. (2001) Zooplankton assemblages and biomass during a 4-period survey in a northern Mediterranean coastal lagoon. Water Research 35(1): 271-283.

Mazzocchi, M. and d'Alcala, M. (1995) Recurrent patterns in zooplankton structure and succession in a variable coastal environment. Ices Journal of Marine Science 52: 679-691.

Mengesha, S., Dehairs, F., Fiala, M. et al. (1998) Seasonal variation of the phytoplankton community structure and nitrogen uptake regime in the Indian Sector of the Southern Ocean. Polar Biology 20(4): 259-272.

M'harzi, A., Tackx, M., Kesaulia, I., Caturao, R., and Podoor, N. (1998) Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone. Journal of Plankton Research 20(11): 2031-2052.

Navarro, J. and Thompson, R. (1995) Seasonal fluctuations in the size spectra, biochemical composition and nutritive value of the seston available to suspension feeding bivalves in a subarctic environment. Marine Ecology Progress Series 125: 95-106.

Mouny, P. and Jauvin, J.-C. (2002) Environmental control of mesozooplankton community structure on the Seine estuary (English Channel). Oceanologica Acta 25: 13-22.

Munk, P. (1997) Prey size spectra and prey availability of larval and small juvenile cod. Journal of Fish Biology 51 (Supplement A): 340-351.

Musaeva, E. and Gagarin, V. (2000) Distribution of zooplankton biomass in the Barents Sea in autumn, 1997. Oceanology 40(4): 532-536.

Mutlu, E. (2001) Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. Marine Biology 138: 329-339.

Nakamura, Y. and Turner, J. (1997) Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? Journal of Plankton Research 19(9): 1275-1288.

Newell, G. and Newell, R. (1977) *Marine plankton: a practical guide*. (5 ed.) London: Hutchinson and Co.

Nielson, A., Pederson, A., and Riisgard, H. (1997) Implications of density driven currents for interaction between the jellyfish (*Aurelia aurita*) and zooplankton in a Danish fjord. Sarsia 82: 297-305.

Nielsen, T. and Sabatini, M.(1996) Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. Marine Ecology Progress Series 139: 79-93.

Ohman, M. and Runge, J. (1994) Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* is the Gulf of St. Lawrence. Limnology and Oceanography 39: 21-36.

Olesen, N. (1995) Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. Marine Ecology Progress Series 124: 63-72.

Paffenhofer, G. A. (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). Journal of Plankton Research 15: 37-55.

Penney, R., McKenzie, C., and Mills, T. (2001) Assessment of the particulate food supply available for mussel (*Mytilus* spp.) farming in a semi-enclosed northern inlet. Estuarine, Coastal and Shelf Science 53, 107-121.

Prins, T., Escaravage, V., Smaal, A. C., and Peeters, J. (1995) Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. Ophelia 41, 289-315.

Rodhouse, P., Roden, C., Hensey, M., and Ryan, T. (1985) Production of mussels, *Mytilus edulis*, in suspended culture and estimates of carbon and nitrogen flow: Killary Harbour, Ireland. Journal of the Marine Biological Association of the U.K. 65: 55-68.

Roff, J., Turner, M., Webber, M and Hopcroft, R. (1995) Bactivory by tropical copepod nauplii: extent and possible significance. Aquatic Microbial Ecology 9: 165-175.

Roman, M. (1984) Utilization of detritus by the copepod *Acartia tonsa*. Limnology and Oceanography 29: 949-959.

Schneider, G. and Behrends, G. (1998) Top-down control in a neritic plankton system by *Aurelia aurita* medusae: a summary. Ophelia 48, 71-82.

Stalder, L. and Marcus, N. (1997) Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. Marine Biology 127: 599-607.

Siokou-Frangou, I., Papathanassiou, E., Lepretre, A., and Frontier, S. (1998) Zooplankton assemblages and influence of environmental parameters on them in a Mediterranean coastal area. Journal of Plankton Research 20(5): 847-870.

Sullivan, B. (1995) How does water column structure influence copepod populations in coastal marine systems? Bulletin of Marine Science 53(1): 240-246.

Tande, K., Drobysheva, S., Nesterova, V. et al (2001) Patterns in the variations of copepod spring abundance in the northeastern Norwegian Sea and Barents Sea in cold and warms years during the 1980s and 1990s. Ices Journal of Marine Science 57(6): 1581-1591.

Timko, P., de Young, B., and Foley, J. (1999) *Observations of currents, temperature and salinity in Charles Arm, Newfoundland* (Rep. No. 99-2). St. John's, NL: Department of Physics and Physical Oceanography, Memorial University of Newfoundland.

Todd, C. and Laverick, M. (1991) *Coastal marine zooplankton: a practical manual for students*. New York: Cambridge University Press.

Wiafe, G. and Frid, C. (1996) Short term temporal variation in coastal zooplankton communities: the relative importance of physical and biological mechanisms. Journal of Plankton Research 18(8), 1485-1501.

Chapter 3: Size distributions of zooplankton communities in Notre Dame Bay

3.1 Introduction

Changes in aquatic particle size distributions have been used as evidence of ecosystem disturbances and changes in ecosystem dynamics such as the change from oligotrophy to eutrophy (Baca and Threlkeld, 2000; Razouls et al, 1994; Sprules and Munawar, 1986; Uye, 1994). Changes in zooplankton size spectra may have important ecosystem consequences given that physiological parameters such as respiration, nitrogen excretion, and growth rates may be weight and body length dependent (Blanco et al, 1998; Conover and Gustavson, 1999; Hirst and Sheader, 1997; Kiorbe and Sabatini, 1995, and references therein). Changes in zooplankton size distribution can therefore affect a wide variety of ecosystem processes including nitrogen cycling, vertical flux of organic matter and size selective predation by larval fish predators.

There is evidence that bivalve farming may affect the zooplankton community composition of coastal inlets in Newfoundland (Chapter 2 of this thesis). There may be a negative impact on the abundance of *Temora* sp. (fall) *Oithona* sp. (summer) and copepod nauplii (summer) and a positive impact on the abundance of *Pseudocalanus* sp. (summer), *Centropages* sp (fall), and harpacticoid copepods (most seasons). It is unknown whether size-based differences in the vulnerability of these taxa to mussel ingestion or mussel induced changes in food particles consumed by zooplankton contribute to these differential impacts or whether there might be additional species-specific effects of mussel feeding on zooplankton community size structure.

The size structure of coastal zooplankton can be subject to control by predation (Schneider, G. and Behrends, G., 1998) but there is very little data on the effects of bivalve predation on zooplankton. It is known that the suspension feeding activities of bivalves can change the size distribution of autotrophic plankton as discussed in Chapter 1 of this thesis. It is also known that changes in nitrogen cycling associated with eutrophication can lead to replacement of larger zooplankton taxa by smaller species such as *Oithona* (Uye, 1994). These eutrophication associated changes in taxa were not observed in this study (Chapter 2).

This study examines the size distribution of zooplankton (>110 μm) at two mussel farms and their reference sites in Notre Dame Bay, Newfoundland to determine if the presence of the mussels affects the size distribution of the zooplankton. The community is divided into < 500μm and > 500μm components as there is generally a trophic separation between these classes. The the shape of the distribution of the former and the mean size of the latter is used to characterize the size distributions at the sites.

3.2 Materials and methods

Field sampling and initial sample preparation was carried out as described in Chapter 2.

3.2.1 Coulter Multisizer® distributions: animals 110-500 500 µm

The size distributions of alcohol preserved samples containing animals < 500 µm were determined using a Coulter Counter Multisizer II® with a 560 µm orifice tube. Samples that passed through a 500 µm mesh filter were subsampled using a Folsom plankton splitter until the counts yielded less than 5% co-incidence on the Multisizer®. Splits ranged from 1/4 to 1/64 depending on the density of the sample. The sub-samples were suspended in filtered sea water (10 µm) collected at the Ocean Science Centre, Logy Bay, Newfoundland. The sample was drawn into the counter with a flow rate of 62 mL min^{-1} with the stirrer set between 3 and 4 to keep the animals in suspension. Counting was stopped when the total number of animals in each 10 µm size interval over 100 µm reached 20. The volume counted was determined by subtracting the volume remaining (measured with a 100mL volumetric cylinder) in the counting vessel from the original (400mL). For approximately 30% of the samples, replicate splits were counted for an average difference in total number counted between splits of approximately 10%.

3.2.2 Image Analysis: animals >500 μm

Image analysis has been accepted as comparable to other methods for determining the size distribution of zooplankton populations (Billones, 1999). The size distributions of large animals were determined using image analysis two weeks or more after transfer to formalin. According to Omori and Ikeda (1984) most size change due to transfer to formalin occurs in the first two weeks of storage. Formalin- preserved samples (>500 μm) were transferred to distilled water (300-400mL) and animals from 10 mL aliquots of the ½ split collected using a Stempel pipette were transferred into 25 mm plastic Petri dishes. Excess water was removed with a pipette covered in mesh.

Photographs of each aliquot were taken with a Pixera Professional® viewfinder. The camera was mounted on a PTEM International® macrovideo zoom lens (18-108, f/2.5-close 34-11-10). Camera-to-image distance was adjusted to approximately 20 cm. giving an image:sample magnification of ~ 40X. A Wild ® base provided dark field illumination of the sample. 1260x 960 pixels images were captured with the Pixera Viewfinder software version 2.6® and saved as black and white Joint Photographic Experts Graphic images (jpeg) in the highest quality possible. Calibration photographs of a ruler were taken under the same conditions as each sample.

Images were then opened and measured with ImagePro 4.0 ® image analysis software. The same set of brightness, contrast and gamma filters were stored in a macro and applied to each sample. Length was determined as in Alcaraz (2003). Size filters were used to prevent the program from measuring dust or other non animal particles. If these particles were still measured, the manual "hide object" function was used to prevent the measurement from being counted in the analysis. The zoom function was used in conjunction with the split function to separate animals as two separate objects when the program could not do so. For each sample 400-600 animals were usually measured. The number of animals measured in replicate 10 ml aliquots were usually within 5% of each other for the total abundance estimates.

3.2.3 Parameterization of size distributions

The small animal size distributions as determined by the Coulter Multisizer® were negative logarithmic functions. Many researchers have used some form of the slope of the size spectra (β_{size}) whether based on biomass or density to characterize pelagic systems (Piontkovski et al, 1995; Razouls et al, 1994; Zhou and Huntley, 1997). The mean (of two tows) frequency distribution for the 100-500 μm class size class for each station were reduced to a log linear regression of the form:

$$\text{Ln}\,[F(\text{size})] = \beta_0 + \beta_{\text{size}}\,\text{Size} + \varepsilon$$

where F(size) is the frequency of animals of each size class and "Size" is the size class given by the Coulter Multisizer II®. In all cases these regressions were significant at α=0.01 and had r^2 greater than 0.70 (This was a better fit than the log-log form of the regression for which a larger proportion of the regressions had an r^2<0.70).

3.2.3 Statistical analysis

β_{size} coefficients and the mean size of large animals for each station sampled were used to compute a Bray-Cutris dissimilarity matrix on which cluster analysis was completed as in Chapter 2 in order to characterize general patterns in the size structure of the zooplankton communities and to determine if samples clustered in patterns of season, location or site based on size parameters.

The average β_{size} coefficient for each station for each of the sites for each of the time periods and the mean size of large animals was used as a response variable for general linear modeling as described in Chapter 2. Power analysis was also conducted for the size parameters in the same manner as in Chapter 2.

3.3 Results

3.3.1 Clustering of stations based on size parameters

Cluster analysis separated the July 2002 CA 51 and CA X3 communities as distinct from other stations. Two other large groups were evident but there was no consistent pattern with respect to season, location or site.

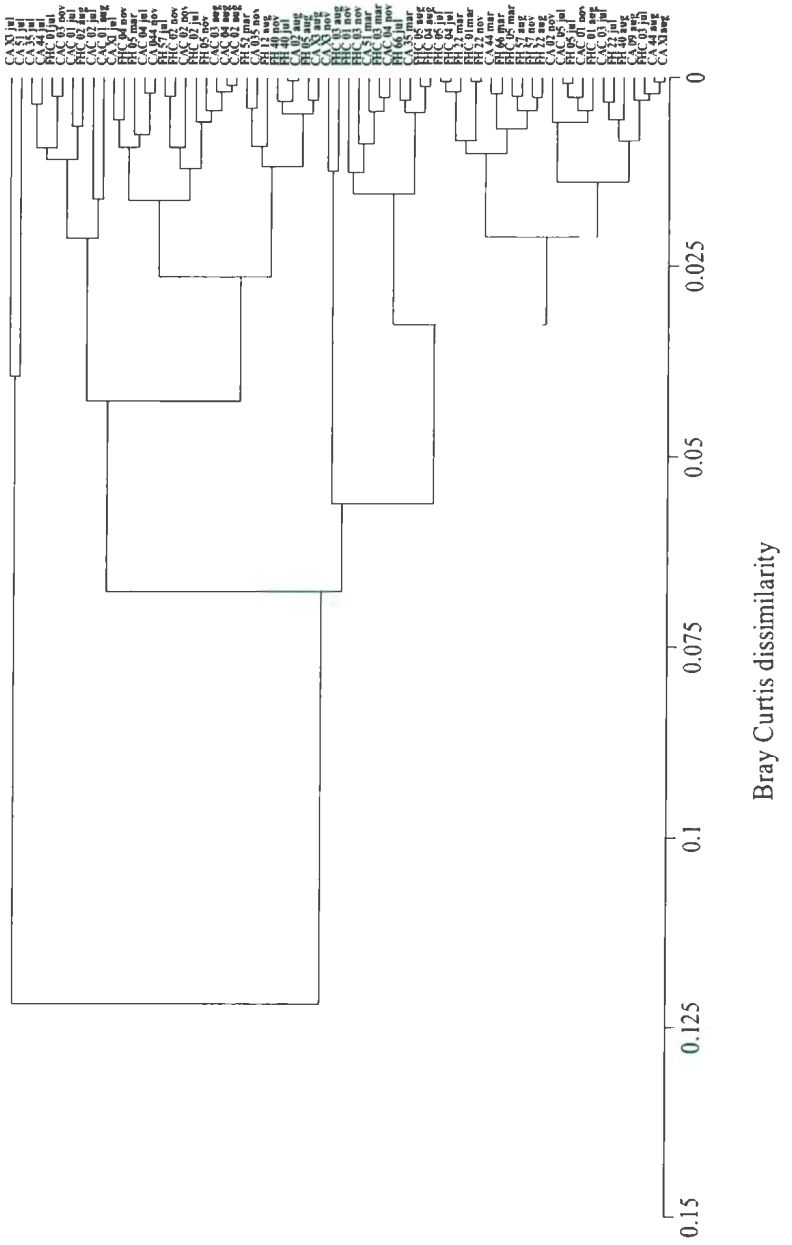

Figure 3.1: UPGMA clustering of stations based on the Bray-Curtis dissimilarity matrix of size parameters (β_{size} and mean size of large animals) "ca" refers to CA farm stations, "cac" refers to CA reference stations, "fh" refers to FH farm stations, and "fhc"refers to FH ref stations. "aug" refers to August 2001, "nov" refers to November 2001, "mar" refers to March 2002 and "jul" refers to July 2002.

3.3.2 Small animal size distributions

The magnitude of β_{size} indicates the steepness of the small animal size distribution. The more negative the β_{size} the more to the left the distribution is shifted, i.e. the smaller size classes are relatively more abundant. In Table 3.1 two extreme community types are evident, being represented by FH farm in March 2002 at the least negative value, and FH farm in August 2001 being the most negative. These two extreme distributions show that less negative slopes are associated with more animals in the 200-400 μm range. The considerable variation in the shapes of the size among stations within sites can be seen in Figures 3.3 to 3.6.

β_{size} varied significantly with season but there were no overall differences between locations in Notre Dame Bay or between farms and references (see Table 3.1). As indicated by the significant interaction terms in Table 3.1, location and site differences occurred in some seasons and not others. In August location ($F_{1, 18}$= 11.46, p= 0.004) was a significant predictor with the CA sites having a less negative β_{size} than FH whereas the farms did not differ from their references ($F_{1, 18}$=0.49, p=0.496). In November neither location ($F_{1, 15}$= 0.56, p=0.471) or site ($F_{1, 15}$=1.60, p=0.230) were significant predictors. In July, location ($F_{1, 19}$= 9.91, p=0.0060) was a significant predictor with CA area having

a more negative β_{size} than the FH area whereas site ($F_{1, 19}$=2.65, p=0.123) was not a significant predictor. In March , locations in Notre Dame Bay were not different ($F_{1, 9}$= 0.27, p=0.617) but FH ref was significantly lower than FH farm at α=0.1 ($F_{1, 6}$=5.72, p=0.062).

Table 3.1: General linear model of β_{size} for the whole data set

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Season	3	0.0005218	0.0003041	0.0001014	4.10	**0.011**
Location	1	0.0000347	0.0000007	0.0000007	0.03	0.868
Site	1	0.0000088	0.0000099	0.0000099	0.40	0.529
Season*Location	3	0.0002692	0.0002963	0.0000988	3.99	**0.012**
Season*Site	3	0.0002111	0.0002627	0.0000876	3.54	**0.021**
Location*Site	1	0.0000685	0.0000685	0.0000685	2.77	0.102
Error	52	0.0012856	0.0012856	0.0000247		
Total	64	0.0023997				

Table 3.2: Mean ± sd of 1000 (β_{size}) of the <500 µm size distribution for each site during each study period. The asterisk indicates a significant difference of a farm from its reference.

Season	CA farm	CA ref	FH farm	FH ref
August, 2001	-18.97±2.44	-22.62±2.53	27.29±3.67	-26.07±5.40
November 2001	-16.86±4.22	-17.06±3.31	-25.05±3.68	-14.80±3.55
March 2002	-15.43±3.43	No data	-13.88±3.13*	-21.24±5.09*
July 2002	-26.20±2.64	-23.72±3.64	-21.73±1.83	-19.93±3.30

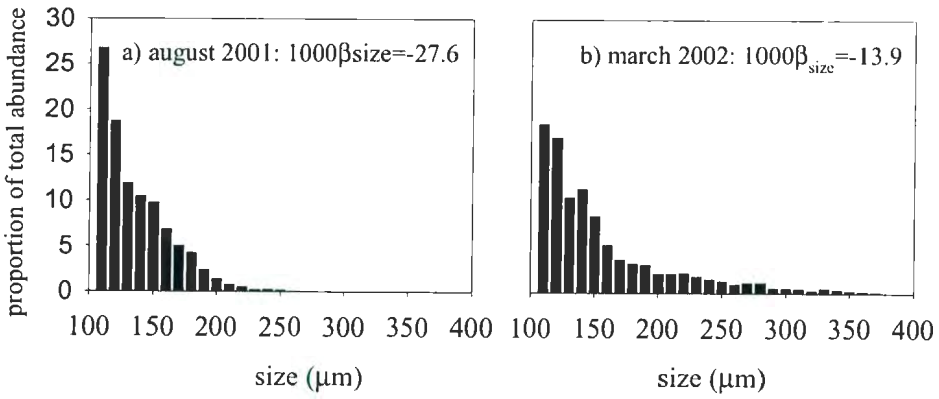

Figure 3.2: Mean size spectra of FH farm in a) August 2001 and b) March 2002 showing maximum and minimum mean β_{size} for sites

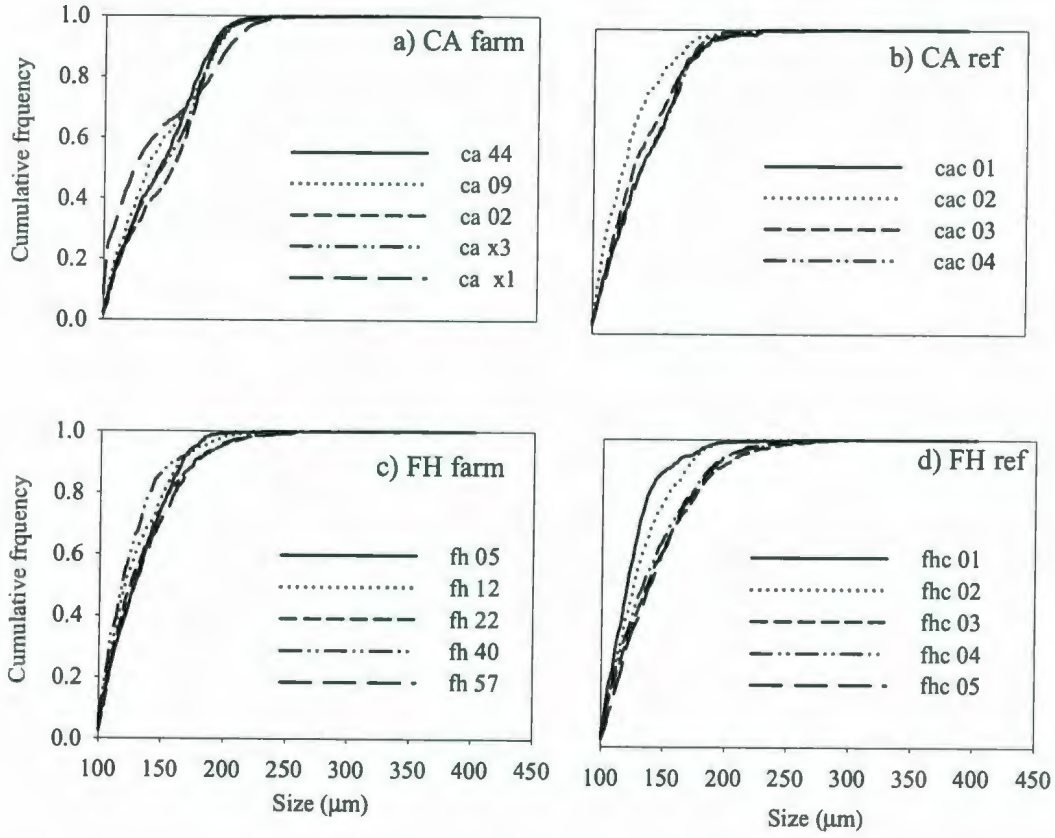

Figure 3.3 (a-d): Cumulative frequency distributions of small animals in August 2001 Each line represents the mean distribution of each station sampled.

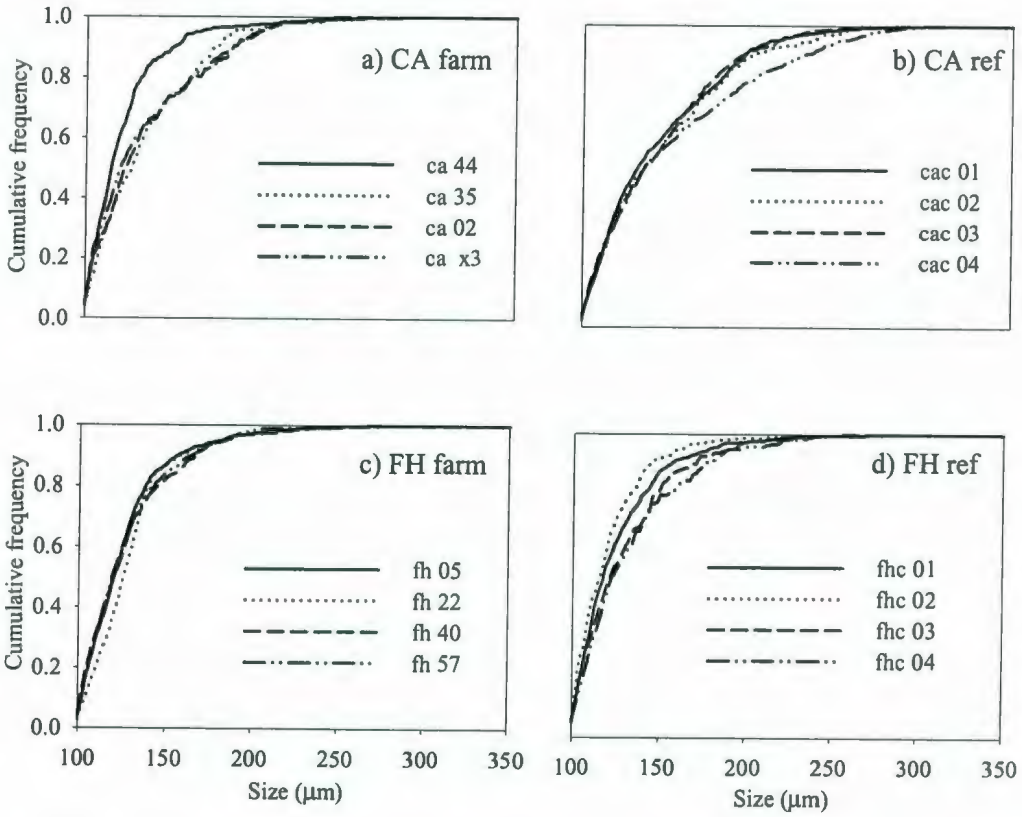

Figure 3.4 (a-d): Cumulative frequency distributions of small animals in November 2001

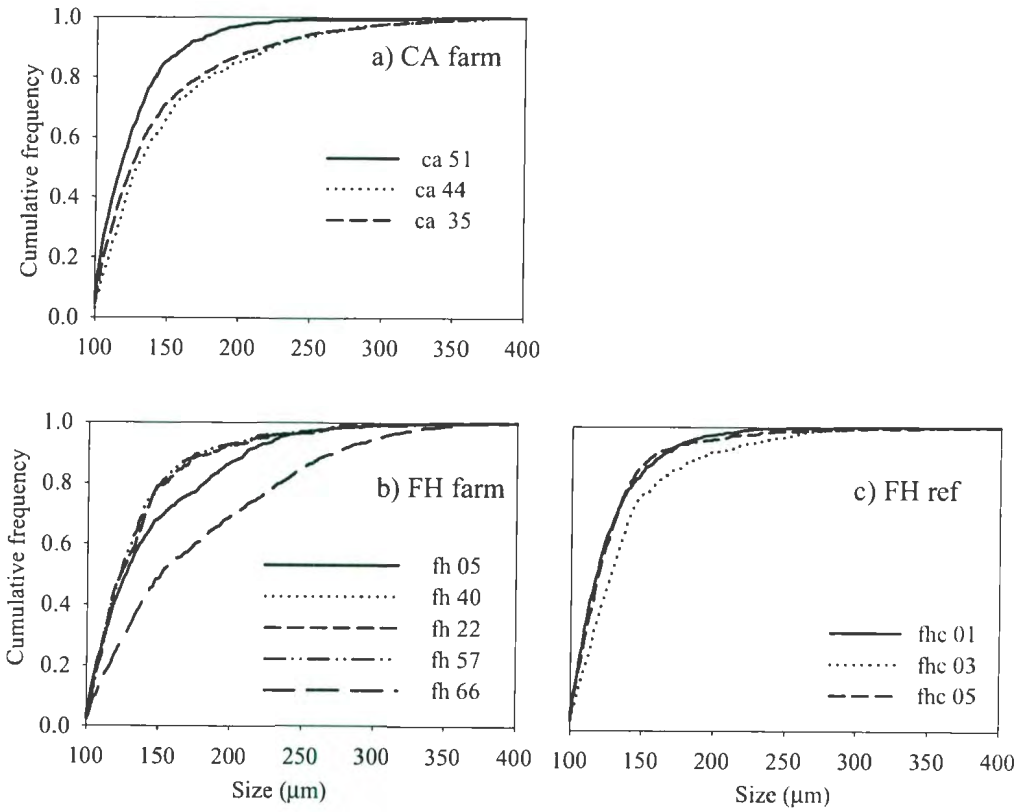

Figure 3.5 (a-d): Cumulative frequency distributions of small animals in March 2002

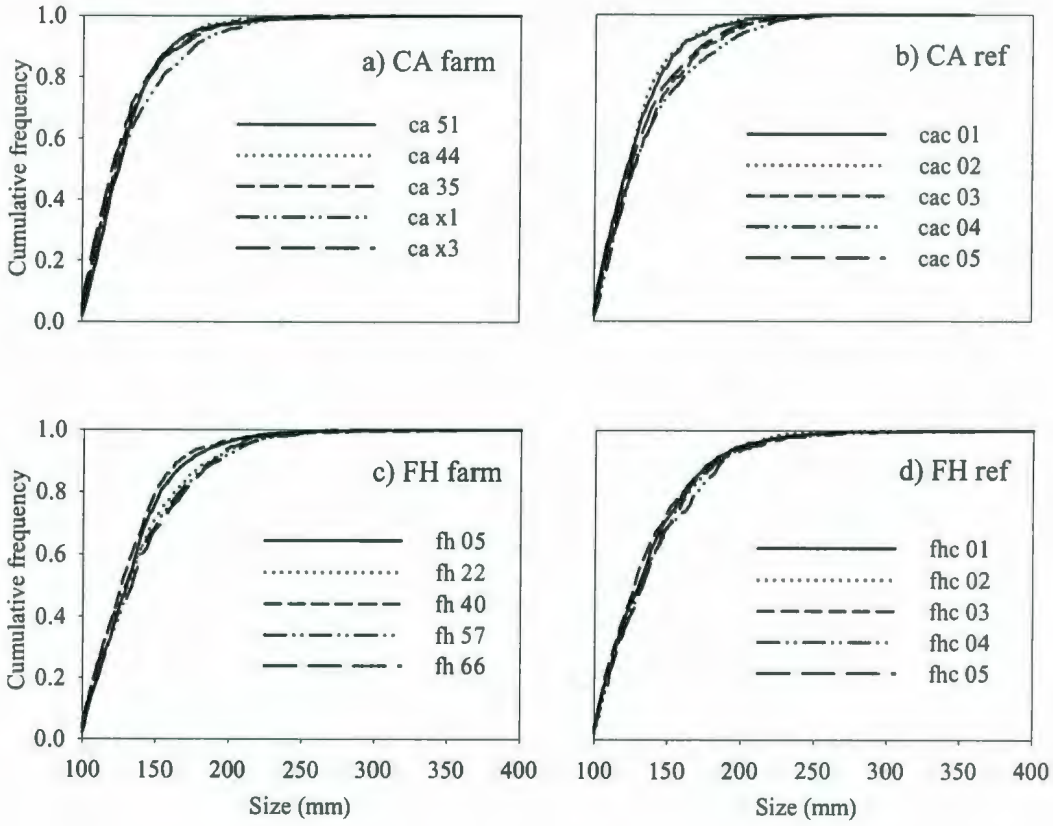

Figure 3.6 (a-d): Cumulative frequency distributions of small animals in July 2002

3.3.3 Large animal size distributions

The mean size of large animals varied seasonally being higher across all sites in March (1123.3±57.1 μm) when the abundance of most major species was lowest (with the exception of harpacticoid copepods) and lowest in July 2002 (1083.4±92.5 μm) when the abundance of most major species was highest (Table 3.3, Table 3.4, Chapter 2 of this thesis). The considerable variation in shape of the size structure can be seen in Figures 3.7-3.10.

The significant Location*Site interaction term in Table 3.3 reflects the difference between CA and FH with respect to the references ($F_{1, 28}$=8.43, p=0.009) but not the farms ($F_{1, 34}$=0.83, p=0.369) . The mean size of large animals was greater in FH compared to CA in August 2001 ($F_{1, 18}$=3.79, p=0.068) and July 2002 ($F_{1, 19}$=8.34, p=0.010). Farms did not differ from their references except for CA farm in August 2001 when the average size of >500 μm animals was ~100 μm higher at the farm than at reference site ($F_{1, 8}$=21.99, p=0.002,).

Table 3.3: General linear model of the mean size of large animals for the whole data set.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Distance	1	26612	14440	14440	2.19	0.144
Season	1	22455	21431	21431	3.26	**0.077**
Location	1	53334	3028	3028	0.46	0.500
Site	1	1304	5145	5145	0.78	0.380
Location*Season	1	3159	2865	2865	0.44	0.512
Site*Season	1	6530	7871	7871	1.20	0.279
Location*Site	1	10541	26084	26084	3.96	**0.051**
Location*Site*Season	1	16823	16823	16823	2.56	0.115
Error	56	368554	368554	6581		
Total	64	509312				

Table 3.4: Mean ±sd of the average size (µm) of large animals in each site and study period. The asterisk indicates a significant difference of a reference from its farm.

Season	**CA farm**	**CA ref**	**FH farm**	**FH ref**
August, 2001	1085.29±28.5*	984.9±36.4*	1087.4±37.8	1119.2±105.1
November 2001	1101.1±113.8	049±104.1	1082.9±65.6	1099.9±111.3
March 2002	1156.5±27.8	No data	1077.2±61.7	1151.0±33.2
July 2002	922.6±78.9	1011.8±75.5	1074.7±66.2	1065.6±85.3

3.3.3 Power analysis of size spectra

The minimum detectable difference in the size parameters for the whole data set based on site was 14% for β_{size} and 5.2% for mean size of large animals. These are relatively small differences and strongly indicate that even very small effects of the farms could have been detected.

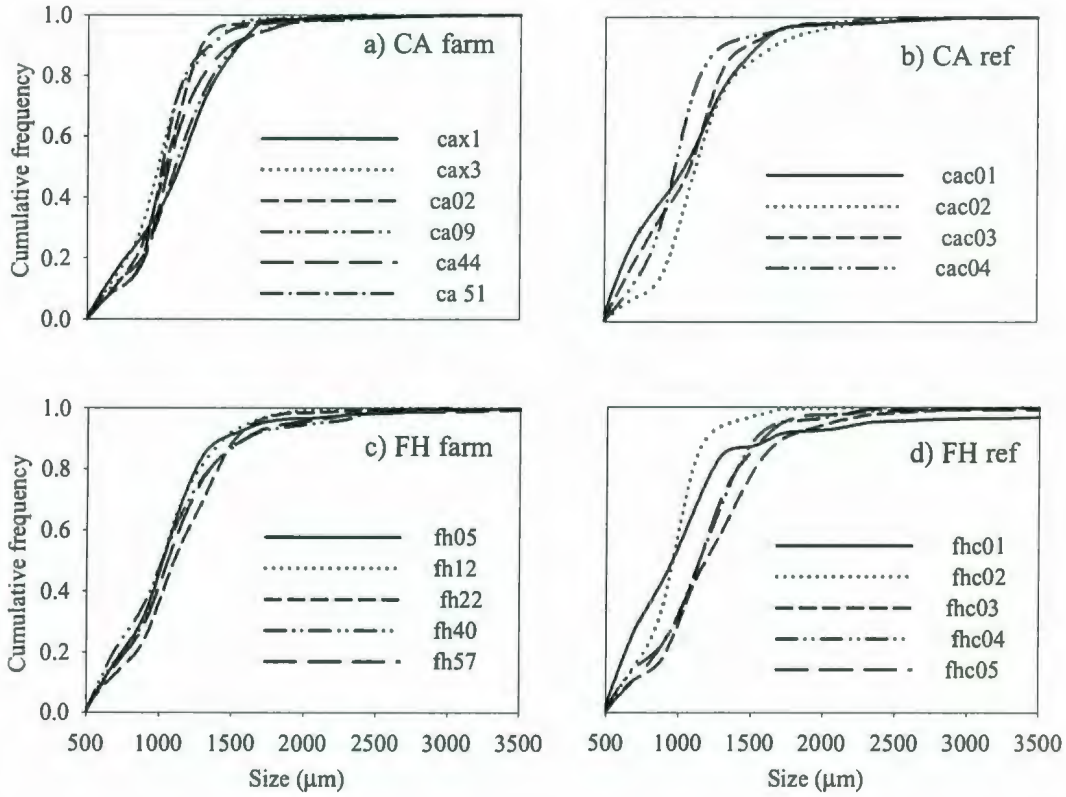

Figure 3.7 (a-d): Cumulative frequency distributions of large animals in August 2001. Each line represents the mean distribution of each station sampled.

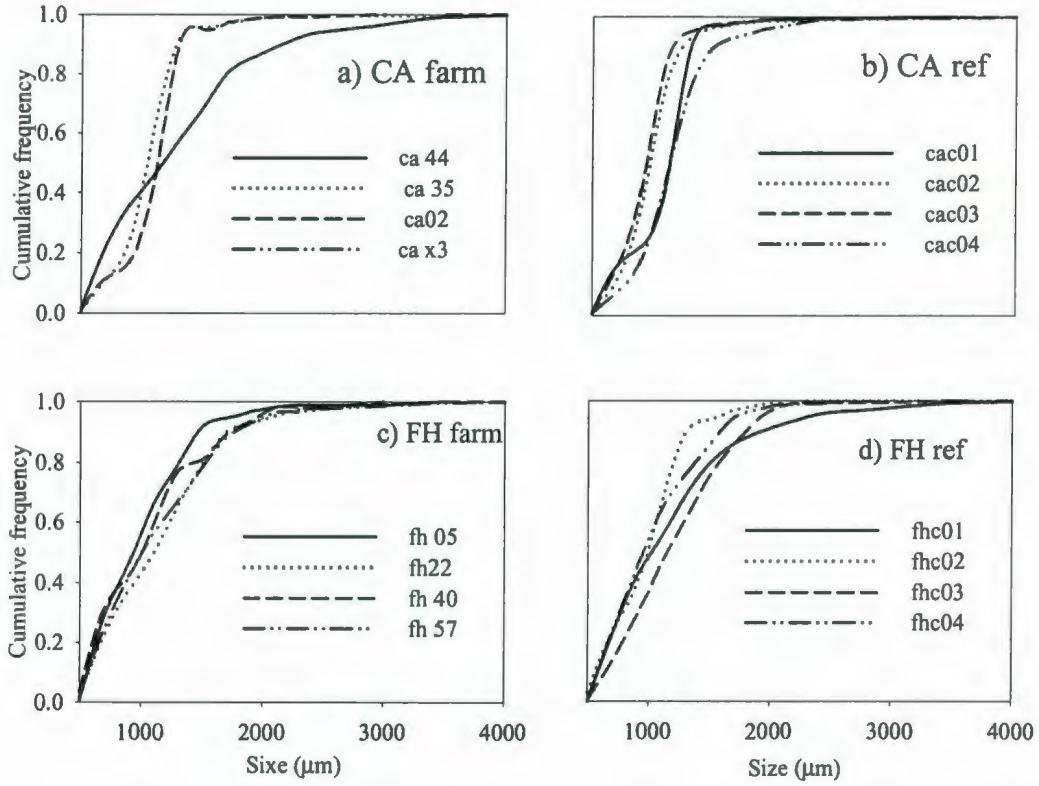

Figure 3.8 (a-d): Cumulative frequency distributions of large animals in November 2001

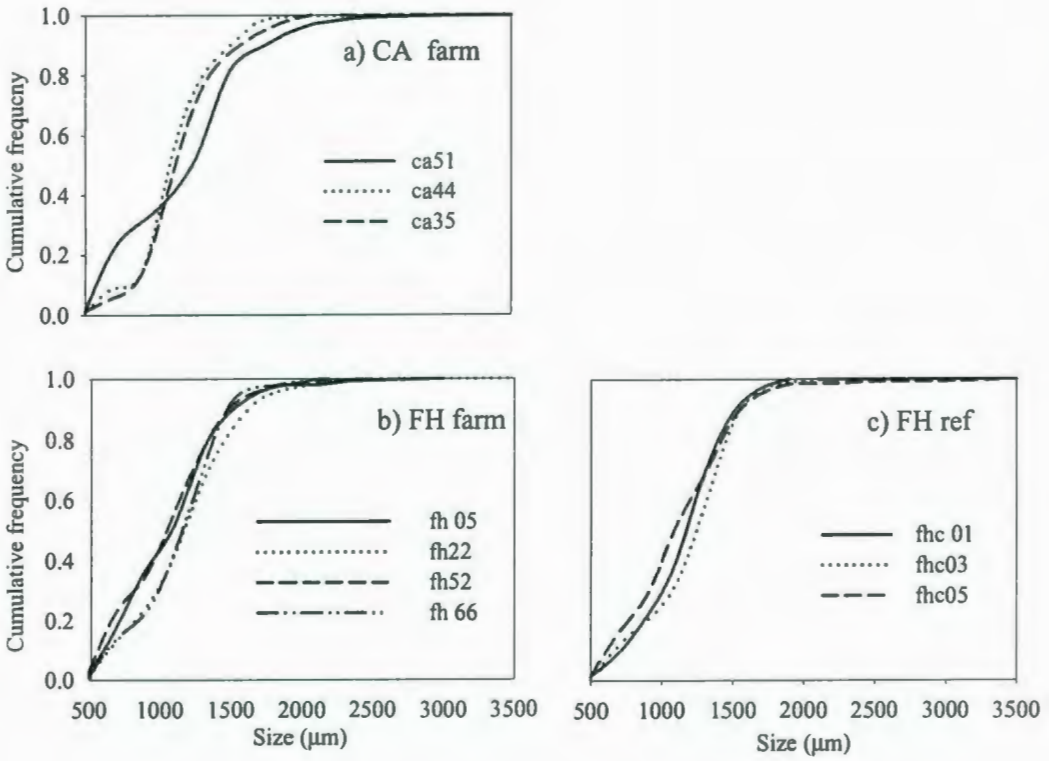

Figure 3.9 (a-d): Cumulative frequency distributions of large animals in March, 2002

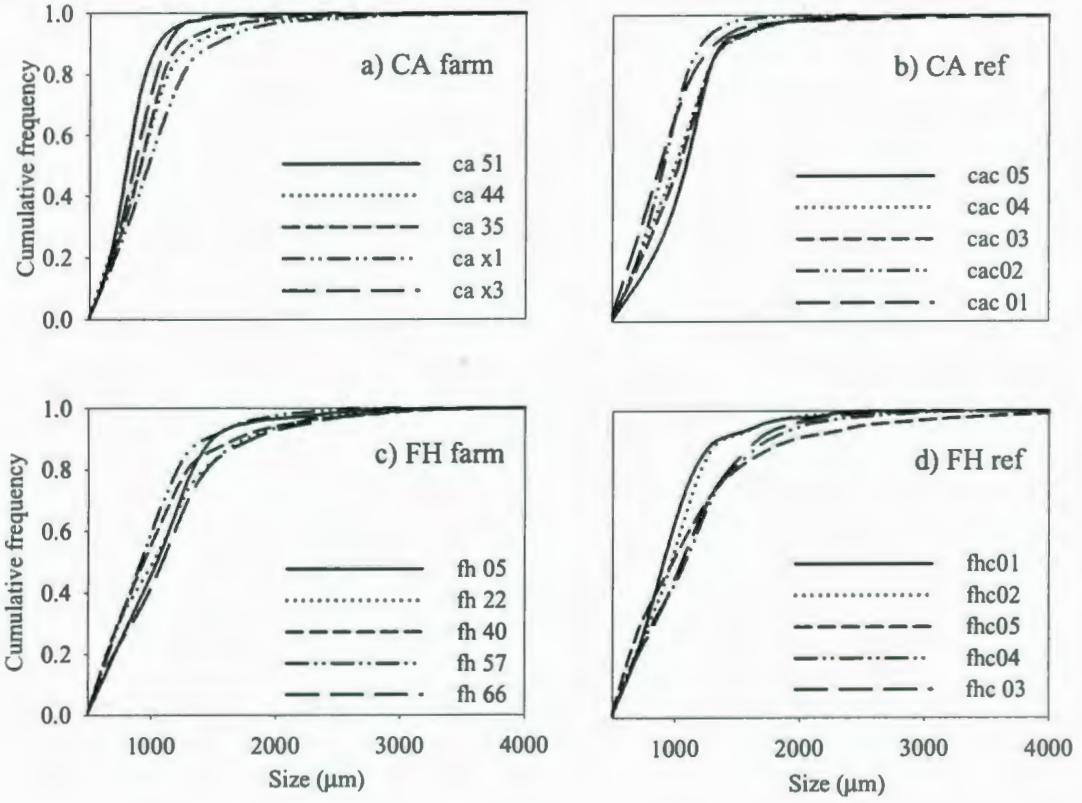

Figure 3.10 (a-d): Cumulative frequency distributions of large animals in July 2002

3.4 Discussion

3.4.1 Effect of mussel farming

While the abundance of some species may be affected (see Chapter 2), the size structure of the zooplankton communities in Notre Dame Bay is not consistently or broadly affected by bivalve farming as indicated by the overall lack of a difference in both size parameters between the farms and their reference sites. The power analysis indicates that relatively small differences could have been detected. Size structure analysis may therefore be of limited utility as a tool in monitoring pelagic impacts of mussels. However, higher resolution temporal coverage and size distributions of individual species are required to be certain of this conclusion. Future studies of this type should also include sampling of sites several weeks apart within the same season to account for possible differences in the timing of cycles of abundance and life stages for the major species involved in the different sites.

There were several instances when the community size structure of a farm was different from its reference site. Mean size of large animals was significantly greater at CA farm compared to its reference site in August 2001.This may reflect the difference in the relative community composition. The relative abundance of *Acartia* sp. was higher ($F_{1,5}$=9.92, p=0.035) at the farm (37%) compared to the reference (19%). The less negative β_{size} in March 2002 at CA and FH farms compared to the FH reference site may also be

related to relative community composition with a higher relative abundance of *Acartia* at the farms (33±11%) compared to FH ref (4.2±4.5%). In addition, *Oithona* sp. was in higher relative abundance at FH ref (56±5%) than at the farms (40± 11%). The latter species tends to be smaller than the former.

3.4.2 Other controls of zooplankton size structure: seasonality, temperature, predators

Biological and physical factors and their interactions must be more important controls of the size structure of zooplankton communities in Notre Dame Bay than bivalve farming. Seasonal temperature changes and the temperature regime in general are important physical controls given that the rates of many physiological processes are temperature dependent. Important related biological factors include the timing of life cycles of dominant zooplankton species and their food, and grazing by other predators.

Season was a significant predictor of the mean size of large animals but not of β_{size}. This does not totally discount temperature as an important control of size structure. The lack of seasonal temperature effect on small animal size structure in this study may be a result of opposite seasonal effects on different species dominant at different times of year i.e. an increase in size in one species may be counteracted by a decrease in the size of another in whole community size analysis. For example, body sizes of *Acartia clausi* and *Oithona* sp. are negatively correlated with increases in temperature (from 5 to 28 °C) while the

length of *Centropages* sp. is positively correlated with temperature (Riccardi and Marriotto,2000). Individual species size distributions are necessary to determine of this was the case for this study.

While predation by *Mytilus* species did not greatly change size spectra, predation by other species may be an important control. Medusae such as *Aurelia* sp. are present in all four of the sites studied and the zooplankton species present in Notre Dame Bay are among those most preyed upon by them (Graham and Kroutil, 2001). Juvenile fish are also important predators of the zooplankton in this area (Grant and Brown, 1997). The timing of the life cycles of both of these groups may be important as the size spectra of the prey animals consumed shifts during their life cycles.

3.4.3 Predominance of small animals

As shown in Chapter 2 of this thesis, most of the mesozooplankton in Notre Dame Bay are < 500 μm and as shown in this chapter, most of this fraction is < 200μm. Notre Dame Bay is a cold water environment. The dominance of small species and individuals of these species runs counter to the paradigm that warmer waters contain smaller copepods than do colder waters (Hopcroft, Roff and Chavez, 2001 and references therein). However, small species tend to predominant in shallow coastal areas Hopcroft et al, 2001). In these areas of Notre Dame Bay, then, the constraints of the shallow and coastal

aspects of the environment may be more dominant in determining community characteristics than the low temperatures.

In shallow coastal waters, Hopcroft et al (2001) suggested that small organisms can dominate in *unproductive* environments because they can exploit the dominant small-celled prey. In *productive* coastal environments the spectra may also be shifted downward due to size selective predation or to the inability of more oceanic plankton to cope with inshore food fields (Hopcroft et al, 2001). Previous work suggests that Notre Dame Bay is a relatively productive environment in general but there are periodic years of low productivity (Penney et al, 2001) and thus both factors might contribute to the size structure. The size efficiency hypothesis (Brooks and Dodson, 1965) can also be applied in that the intensity of predation by medusae and juvenile fish (in addition to bivalves) may eliminate large forms, causing small plankton to become dominant.

3.4.4 Size spectra and productivity

In general, periods of steepest β_{size} coincided with increased abundance of > 500 µm animals and vice versa. This suggests general shifts from periods of dominance by nauplii and younger juvenile stages, which are associated with more steep β_{size} and lower abundance of large animals to periods with more animals in late juvenile and adult stages which are associated with periods of less steep β_{size} and an increased abundance and size

of animals > 500 μm. Steep size spectra slopes (i.e. more negative β_{size}) of aquatic particles are usually observed in locations and during times of highest productivity (Piontkovski, Williams and Melnik, 1995). In warm waters β_{size} is usually steeper in late summer and less steep in winter (Gilabert, 2001). In Note Dame Bay, negative β_{size} would indicate highest zooplankton productivity in mid to late summer for CA sites with additional high periods in fall for FH farm and March for FH reference.

In general, in this area of NDB, large blooms occur in the spring, (sometimes starting under the land fast ice) and secondary blooms occur in fall (Penney et al, 2001). Although there is a lack of synchronicity in the cycles of low and high β_{size} among sites, more negative values were associated with the highest abundances of copepod nauplii in the mid to late summer. Higher β_{size} occurred in March 2002 when the abundance of most major taxa was lowest and when the community was composed primarily of *Acartia* sp, *Centropages* sp. and *Oithona* sp. This lag between primary production and secondary production is common in coastal areas where cold spring water temperatures limit the rate of development. Again, higher resolution temporal coverage is needed to determine the life cycle characteristics of zooplankton in this area. At this time we do not know how many generations per year are produced by each of the major taxa and if there is a time lag in production of young among any of the sites or locations in Notre Dame Bay.

The β_{size} was relatively negative at FH farm in November as well as in the warmer months. This is not the case for its reference site or for the CA sites. Two of the main differences in community composition between FH farm and its reference site in November are that FH farm has a higher abundance of harpacticoid copepods than the reference site and the reference has a higher relative abundance of *Oithona* sp. and polychaete larvae than the farm (chapter 2 of this thesis). This may account for the difference. The other possibility is that there was higher production of copepods stimulated by a fall bloom which was missed by the sampling program at the other sites due to a lack of synchronicity in the timing or duration of the bloom. This is more likely a factor in the comparisons of CA and FH and less likely in comparisons of the sites within the FH area.

In summary, given the species-specific effects on zooplankton abundance by mussel farms and the lack of consistent effects on the total abundance and size spectra, it can may be concluded that inherent aspects of this coastal zone such as temperature or primary productivity cycles control abundance and size structure while the individual species abundance may be subject to control by bivalves. A temporally comprehensive study of the size spectra of individual zooplankton and phytoplankton species at these sites in addition to mussel feeding experiments (on different zooplankton taxa and size classes) is needed to clarify and confirm these observations.

3.5 References

Alcaraz, M., Saiz, E., et al. (2003) Estimating zooplankton biomass through image analysis. Marine Biology DOI 10.1007/s00227-003-1094-8.

Baca, R. and Threlkeld, S. (2000) Using size distributions to detect nutrient and sediment effects within and between habitats. Hydrobiologia 435: 197-211.

Billones, R., Tackx, M. et al. (1999) Image analysis as a tool for measuring particle matter concentrations and gut content, body size and clearance rates of estuarine copepods: validation and application. Journal of Marine Systems 22: 179-194.

Blanco, J., Quinones, R. Guerrero, F and Rodriguez, J. (1998) The use of biomass specta and alometric relations to estimate respiration of planktonic communities. Journal of Plankton Research 20: 887-900.

Brooks, J. and Dodson, S. (1965) Predation, body size and composition of plankton. Science 150: 28-35.

Conover, R. and Gustavson, K. (1999) Soures of urea in arctic seas: zooplankton metabolism. Marine Ecology Progress Series 179: 41-54.

Gilabert, J. (2001) Short term variability of the planktonic size structure in a Mediterranean coastal lagoon. Journal of Plankton Research 23(2): 219-226.

Graham, W. and Kryoutil, R. (2001) Size-based prey selectivity and dietary shifts in the jellyfish *Aurelia aurita*. Journal of Plankton Research 23(1): 67-74.

Hirst, A. and Sheader, M. (1997) Are *in situ* weight-specific rates of body size independent in marine planktonic copepods? A re-analysis of the global syntheses and a new empirical model. Marine Ecology Progress Series 154: 155-165.

Hopcroft, R., Roff, J., and Chavez, F. (2001). Size paradigms in copepod communtiies: a re-examination. Hydrobiologia 453/454:133-141.

Kiorbe, T. and Sabatini, M. (1995) Scaling of fecundity, growth and development in marine planktonic copepods. Marine Ecology Progress Series 120: 285-298.

Omori, M. and Ikeda, T. (1984) *Methods in marine zooplankton ecology*. New York. Wiley-Interscience.

Penney, R., McKenzie, C., and Mills, T. (2001) Assessment of the particulate food supply available for mussel (*Mytilus* spp.) farming in a semi-enclosed northern inlet. Estuarine, Coastal and Shelf Science 53: 107-121.

Piontkovski, S., Williams, R. and Melnik, T. (1995) Spatial heterogeneity, biomass and size structure of plankton of the Indian Ocean: some general trends. Marine Ecology Progress Series 117: 219-227.

Razouls, S., De Bovee, F et al. (1994) Are size spectra of mesozooplankton a good tag for characterizing pelagic ecosystems? Vie et Milieu 44(1): 59-68.

Riccardi, N. and Marriotto, L. (2000) Seasonal variation in copepod body length: a comparison between different species in the Lagoon of Venice. Aquatic Ecology 34: 243-252.

Schneider, G. and Behrends, G. (1998) Top-down control in a neritic plankton system by *Aurelia aurita* medusae: a summary. Ophelia 48: 71-82.

Sprules, W. and Munawar. (1986) Plankton size spectra in relation to ecosystem productivity, size and perturbation. Canadian Journal of Fisheries and Aquatic Sciences 43: 1789-1794.

Uye, S. (1994) Replacement of large copepods with small ones with eutrophication of embayments: causes and consequences. Hydrobiologia 292/293: 513-519.

Zhou, M. and Huntley, M. (1997) Population dynamics theory of plankton based on biomass spectra. Marine Ecology Progress Series 159: 61-73.

Chapter 4: Summary

4.0 Summary

Bivalve mollusks such as *Mytilus* sp affect the benthic and pelagic ecosystems in which they are located. In the pelagic system, mussels may reduce seston and chlorophyll levels and sometimes change the composition of the autotrophic community through various positive and negative feedback loops. Relatively little is known about the role of bivalves in shaping the mesozooplankton community and even less is known about how bivalve farming may change it.

Results of this study suggest that the composition of the coastal zooplankton community may be affected by the addition of a large biomass of bivalves. In Notre Dame Bay, however, general characteristics may be under broader environmental or biological controls. Monitoring changes in the zooplankton community caused by bivalve aquaculture may therefore be better centered on community composition rather than on parameters such as community size structure, total abundance and biomass.

The impact of mussel farming on specific zooplankton groups was restricted to certain sampling periods. *Acartia* sp .and *Pseudocalanus* sp. (summer) *Centropages* sp (fall) and harpacticoid copepods (most seasons) were more abundant at the farms than at their reference sites (fall) while *Temora* sp. (fall), *Oithona* sp (summer) and copepod nauplii (summer) were more abundant at the reference sites. The different impacts on zooplankton may reflect different abilities to utilize the food or physical environment of the farms or in their vulnerability to ingestion by or competition for food with mussels.

The impacts of these changes are unknown at this time but may included reduced or increased export of organic matter to the benthos depending on season and changes in the microbial food web.

The overall size structure and total abundance of zooplankton were not affected by the presence of the mussel farms. This suggests that the effects of the farms on the groups discussed above are not based on size. It is unknown whether the size spectra of individual species differ between the farms and their references. Biological factors such as the timing of cycles of primary production and predation by organisms other than bivalves, as well as inherent physical aspects of this coastal environment may be more important controls of total zooplankton abundance and size structure than the presence or absence of mussel farms.

A key general feature of the zooplankton communities of Notre Dame Bay shared with many other coastal waters is the predominance of few common species such as *Acartia* sp. and *Oithona* sp. and of smaller size fractions. *Oithona*, *Pseudocalanus*, polychaete larvae and harpacticoid copepods were identified as dominating colder season communities while *Centropages*, *Acartia*, *Temora* and copepod nauplii were associated with warmer seasons. This strong seasonal component in the total and species -specific abundance is also common feature of coastal environments.

Another feature common to cold coastal waters is the lag between primary and secondary zooplankton production. The higher abundance small animals, especially copepod nauplii, and the steep β_{size} in summer months indicate that for the bulk of copepods in Notre Dame Bay, the production of juveniles occurs after the spring bloom. Some species must produce nauplii at other times as nauplii were present (albeit in low numbers) during all study periods. The largest animals >500μm occurred in March when the relative contribution of large animals to total abundance was highest. These may have been the result of production after the fall bloom but this study lacks the temporal coverage to be certain about this conclusion.

Inshore Note Dame Bay has a notable set of physical characteristics in its relatively low latitude yet relatively cold temperatures, winter ice cover and its relative freedom from widescale, anthropogenic pollution impacts. Very few studies exist on the zooplankton communities of such areas. This work suggests that the zooplankton community of this area may be affected by mussel farming. This study also suggest that a comprehensive study of the impacts of mussel culture on the pelagic system, including zooplankton, would reveal much about the role of bivalves in shaping coastal ecosystems in general.

5.0 References

References

Alcaraz, M., Saiz, E., et al. (2003) Estimating zooplankton biomass through image analysis. Marine Biology DOI 10.1007/s00227-003-1094-8.

Asmus, R. and Asmus, H. (1991) Mussel beds: limiting or promoting phytoplankton? Journal of Experimental Marine Biology and Ecology 148: 215-232.

Arashkevich, E., Wassmann, P. et al. (2002) Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. Journal of Marine Systems 38: 125-145.

Archambault, P., Roff, J., Bourget, E., Bang, B., and Ingram, G. (1998) Nearshore abundance of zooplankton in relation to coastal topographic heterogeneity and the mechanisms involved. Journal of Plankton Research 20: 671-690.

Baca, R. and Threlkeld, S. (2000) Using size distributions to detect nutrient and sediment effects within and between habitats. Hydrobiologia 435: 197-211.

Barranguet, C. (1997). The role of microphytobenthic primary production in a Mediterranean mussel culture area. *Estuarine, Coastal and Shelf Science 44:* 753-765.

Baudinet, D., Alliot, E., Berland, B., Grenz, C., Plante-Cuny, MR., Plante, R. et al. (1990) Incidence of mussel culture on biogeochemical fluxes at the sediment-water interface. Hydrobiologia 207: 187-196.

Bayne B. and Scullard C. (1977) Rates of nitrogen excretion by species of *Mytilus* (Bivalvia: Mollusca). Journal of the Marine Biological Association of the UK 57: 355-369.

Beaumont, K., Plummer, A., Hosie, G., and Ritz, D. (2001). Production and fate of faecal pellets during summer in an East Antarctic fjord.Hydrobiologia 453/454: 55-65.

Billones, R., Tackx, M. et al. (1999) Image analysis as a tool for measuring particle matter concentrations and gut content, body size and clearance rates of estuarine copepods: validation and application. Journal of Marine Systems 22: 179-194.

Blanco, J., Quinones, R. Guerrero, F and Rodriguez, J. (1998) The use of biomass spectra and allometric relations to estimate respiration of planktonic communities. Journal of Plankton Research 20: 887-900.

Brooks, J. and Dodson, S. (1965) Predation, body size and composition of plankton. Science 150: 28-35.

Bucklin, A., Kaartvedt, S., Guarnier, M., and Goswami, U. (2000) Population genetics of drifting (*Calanus* spp.) and resident (*Acartia clausii*) plankton in Norwegian fjords. Journal of Plankton Research 22(7): 1237-1251.

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., and Duarte, C. (2001) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. Journal of Plankton Research 23(3): 319-331.

Chamberlain, J., Fernandes, T., Read, P., Nickell, T., and Davies, I. (2001) Impacts of biodeposits from suspended mussel (*Mytilus edulis* L.) culture on the surrounding surficial sediments. ICES Journal of Marine Science 58: 411-416.

Clemens, T., Couturier, C., Parsons, G., and Dabinett, P. (2000) *Environmental characteristics of Newfoundland shellfish farms for 1995-1999: ACERA mussel project #1* St. John's, NL: Memorial University of Newfoundland.

Cloern, J. (1982) Does the benthos control phytoplankton biomass in South San Francisci Bay. Marine Ecology Progress Series 9: 191-202.

Conover, R. and Gustavson, K. (1999) Sources of urea in arctic seas: zooplankton metabolism. Marine Ecology Progress Series 179: 41-54.

Cranford, P. and Hill, P. (1999) Seasonal variation in food utilization by the suspension feeding bivalve molluscs *Mytilus edulis* and *Placopectan magellanicus*. Marine Ecology Progress Series 190: 223-239.

Crocker, K. (1998) *Tracking and growth of larvae of the giant scallop, Placopectan magellanicus (Gmelin, 1791) on a scallop farm in Notre Dame Bay, Newfoundland.* Master of Science Aquaculture, Memorial University of Newfoundland.

Dahlback, B. and Gunnarsson, l. (1981) Sedimentation and sulfate reduction under a mussel culture. Marine Biology: 269-275.

Dalley, E., Anderson, J. and Davis, D. Plankton and nekton of the northeast Newfoundland shelf and Grand Banks in 1998. Canadian Stock Assessment Secretariat Research Document 99/142.

Dame, R., Dankers, N., Prins, T., Jongsma, H., and Smaal, A. (1991) The influence of mussel beds in the Western Wadden Sea and the Eastern Scheldt estauries. Estuaries 14(2): 130-138.

Dankers, N. and Zuidema, D. (1995) The role of the mussel (*Mytilus edulis* L.) and mussel culture in the Dutch Wadden Sea. Estuaries 18(1A):71-80.

Davenport, J., Smith, R., and Packer, M. (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Marine Ecology Progress Series 198: 131-137.

Davis, C. (1982) A preliminary quantitative study of the zooplankton from Conception Bay, Insular Newfoundland, Canada. Int.Revue.ges.Hydrobiol. 67(5): 713-747.

Davis, C. (1987) Predatory control of copepod seasonal cycles on Georges Bank. Marine Biology. 82: 31-40.

Falkenhaug, T., Tande, K., and Timonin, A. (1997) Spatio-temporal patterns in the copepod community in Malangen, northern Norway. Journal of Plankton Research 19(4): 449-468.

Gaard, E. (1999) The zooplankton community structure in relation to its biological and physical environment on the Faroe shelf, 1989-1997. Journal of Plankton Research 21(6): 1133-1152.

Gagnon, M. and Lacroix, G. (1983) The transport and retention of zooplankton in relation to a sill in a tidal estuary. Journal of Plankton Research 5(2): 289-303.

Gallienne, C. and Robins, D. (2001) Is *Oithona* the most important copepod in the world's oceans? Journal of Plankton Research 23(12): 1421-1433.

Garstecki, T., Wickham, S., and Arndt, H. (2002) Effects of experimental sediment resuspension on a coastal planktonic microbial food web. Estuarine, Coastal and Shelf Science 55: 751-762.

Gilabert, J. (2001) Short term variability of the planktonic size structure in a Mediterranean coastal lagoon. Journal of Plankton Research 23(2): 219-226.

Gilbert, F., Souchu, P., Bianchi, M., and Bonin, P. (1997) Influence of shellfish farming activities on nitrification, nitrate reduction to ammonium and denitrification at the water sediment interface of the Thau lagoon, France. Marine Ecology Progress Series 151: 143-153.

Gonzalez, H. and Smetacek, V. (1994) The possible role of the cyclopoid copepod *Oithona* in retarding the vertical flux of zooplankton faecal material. Marine Ecology Progress Series 113: 233-246.

Gonzalez, H., Kurbjewit, F., Bathmann, U. (1994) Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January-February 1991. Polar Biology 14: 331-342.

Gowen, R., McCullough, G., Kleppel, G., Houchin, L., and Elliot, P. (1999) Are copepods important grazers of the spring phytoplankton bloom in the western Irish sea. Journal of Plankton Research 21(3): 465-483.

Graham, W. and Kroutil, R. (2001) Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. Journal of Plankton Research 23(1): 67-74.

Grant, S. and Brown, J. (1998) Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland.Canadian Journal of Fisheries and Aquatic Sciences 55: 1307-1316.

Grant, J., Stenton-Dozey, J., Monteiro, P., Pitcher, G., and Heasman, K. (1998) Shellfish culture in the Benguela system: a carbon budget of Saldanha Bay for raft culture of *Mytilus galloprovincialis*. Journal of Shellfish Research 17(1): 41-49.

Grant, J., Hatcher, A., Scott, D., Pockington, P., Schaffer, C., and Winters, G. (1995) A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. Estuaries 18(1A): 124-144.

Green, R. (1979) *Sampling design and statistical methods for environmental biologists*. New York: John Wiley and Son.

Green, S., Visser, A., Titelman, J., and Kiorbe, T. (2003) Escape responses of copepod nauplii in the flow field of the blue mussel, *Mytilus edulis*. Marine Biology 142(4): 727-733.

Harvey, M., Therriault, J.-C., and Simard, N. (2001) Hydrodynamic control of late summer species composition and abundance of zooplankton in Hudson Bay and Hudon Strait (Canada). Journal of Plankton Research 23(5):481-496.

Hatcher, A., Grant, J., and Schofield, B. (1994) Effects of suspended mussel culture *(Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. Marine Ecology Progress Series 115: 219-235.

Hirst, A. and Sheader, M. (1997) Are *in situ* weight-specific rates of body size independent in marine planktonic copepods? A re-analysis of the global syntheses and a new empirical model. Marine Ecology Progress Series 154: 155-165.

Hopcroft, R., Roff, J., and Chavez, F. (2001) Size paradigms in copepod communtiies: a re-examination. Hydrobiologia 453/454:133-141.

Horsted, S., Nielson, T., Pock-Steen, J., and Koefoed Bjorernsen, P. (1988) Regulation of zooplankton by suspension-feeding bivalves and fish in estuarine enclosures. Marine Ecology Progres Series 48(3): 217-224.

Jenkins, G., Walker-Smith, G., and Hamer, P. (2002). Elements of habitat complexity that influences harpacticoid copepods associated with seagrass beds in a temperate bay. Oecologia 131: 598-605.

Kaiser, M., Laing, I., Utting, S., and Burnell, G. (1998) Environmental impacts of bivalve mariculture. Journal of Shellfish Research 17(1): 59-66.

Kaspar, H., Gillespie, P., Boyer, I., and MacKenzie, A. (1985) Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. Marine Biology 85:127-136.

Kautsky, N. and Evans, S. (1987) Role of the biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. Marine Ecology Progress Series 38: 201-212.

Kimmerer, W. and McKinnon, A. (1985. A comparative study of the zooplankton in two adjacent embayments, Port Phillip and Westernport bays, Australia. Estuarine, Coastal and Shelf Science 21(2): 145-159.

Kiorbe, T. and Mohlenberg, F. (1981) Particle selection in suspension feeding bivalves. Marine Ecology Progress Series 5: 291-296.

Kiorbe, T. and Sabatini, M. (1995) Scaling of fecundity, growth and development in marine planktonic copepods. Marine Ecology Progress Series 120: 285-298.

Kiorbe, T. Saiz, E. and Viitasalo, M. (1996) Prey switching behavior in the planktonic copepod *Acartia tonsa*. Marine Ecology Progress Series 143: 65-75.

Kleppel, G. (1992) Environmental regulation of feeding and egg production by *Acartia tonsa* off Southern California . Marine Biology 112(57): 65.

Lam-Hoi, T. and Rougier, C. (2001) Zooplankton assemblages and biomass during a 4-period survey in a northern Mediterranean coastal lagoon. Water Research 35(1): 271-283.

Loo, L. and Rosenberg, R. (1989) Bivalve suspension feeding dynamics and benthis-pelagic coupling in a eutrophicated marine bay. Journal of Experimental Marine Biology and Ecology 130: 253-276.

Mallin, M. and Paerl, H. (1994) Planktonic trophic transfer in an estuary: seasonal, diel and community structure effects. Ecology 75(8): 2168-2184.

Mattsson, J. and Linden, O. (1983) Benthic macrofauna succession under mussels, *Mytilus edulis* L. cultured in hanging long lines. Sarsia 68: 97-102.

M'harzi, A., Tackx, M., Kesaulia, I., Caturao, R., and Podoor, N. (1998) Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone. Journal of Plankton Research 20(11): 2031-2052.

Mattsson, J. and Linden, O. (1983) Benthic macrofauna succession inder mussels, *Mytilus edulis* L. cultured in hanging long lines. Sarsia 68: 97-102.

Mazouni, N., Gaertner, J. C., and Deslous-Paoli, J. M. (1998) Influence of oyster culture on water column characteristics in a coastal lagoon (Thau, France). Hydrobiologia 373/374: 149-156.

Mazzocchi, M. and D'Alcala, M. (1995) Recurrent patterns in zooplankton structure and succession in a variable coastal environment. ICES Journal of Marine Science 52(3-4): 679-691.

Mengesha, S., Dehairs, F., Fiala, M. et al. (1998) Seasonal variation of the phytoplankton community structure and nitrogen uptake regime in the Indian Sector of the Southern Ocean. Polar Biology 20(4): 259-272.

Mirto, S., La Rosa, T., Danovaro, R., and Mazzola, A. (2000) Microbial and meiofaunal response to intensive mussel-farm biodeposition in coastal sediments of the Western Mediterranean. Marine Pollution Bulletin 40(3): 244-252.

Mohlenberg, F. and Riisgard, H. (1978) Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 22(15): 31.

Mouny, P. and Jauvin, J.-C. (2002) Environmental control of mesozooplankton community structure on the Seine estuary (English Channel). Oceanologica Acta 25: 13-22.

Munk, P. (1997) Prey size spectra and prey availability of larval and small juvenile cod. Journal of Fish Biology 51 (Supplement A): 340-351.

Musaeva, E. and Gagarin, V. (2000) Distribution of zooplankton biomass in the Barents Sea in autumn, 1997. Oceanology 40(4): 532-536

Mutlu, E. (2001) Distribution and abundance of the moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. Marine Biology 138: 329-339.

Nakamura, Y. and Turner, J. (1997) Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? Journal of Plankton Research 19(9): 1275-1288.

Navarro, J. and Thompson, R. (1995) Seasonal fluctuations in the size spectra, biochemical composition and nutritive value of the seston available to suspension feeding bivalves in a subarctic environment. Marine Ecology Progress Series 125: 95-106.

Newell, C., Shumway, S., Cucci, T., and Selvin, R. (1989) The effect of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758, at bottom culture sites in Maine. Journal of Shellfish Research 8: 187-196.

Newell, G. and Newell, R. (1977) *Marine plankton: a practical guide*. (5 ed.) London: Hutchinson and Co.

Nielsen, T. and Sabatini, M. (1996) Role cyclopoid copepods *Oithona* spp. in North Sea plankton communities. Marine Ecology Progress Series 139(1-3): 79-93.

Nielson, A., Pederson, A., and Riisgard, H. (1997) Implications of density driven currents for interaction between the jellyfish (*Aurelia aurita*) and zooplankton in a Danish fjord. Sarsia 82: 297-305.

Noren, F., Haamer, J., and Lindahl, O. (1999) Changes in the plankton community passing a *Mytilus edulis* mussel bed. Marine Ecology Progress Series 191: 187-194.

Ogilvie, S., Ross, A., and Schiel, D. (2000) Phytoplankton biomass associated with mussel farms in Beatrix Bay, New Zealand. Aquaculture 181: 71-80.

Ohman, M. and Runge, J. (1994) Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* is the Gulf of St. Lawrence. Limnology and Oceanography 39: 21-36.

Olesen, N. (1995) Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. Marine Ecology Progress Series 124: 63-72.

Omori, M. and Ikeda, T. (1984) *Methods in marine zooplankton ecology*. New York. Wiley-Interscience.

Paffenhofer, G. A. (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). Journal of Plankton Research 15: 37-55.

Penney, R., McKenzie, C., and Mills, T. (2001) Assessment of the particulate food supply available for mussel (*Mytilus* spp.) farming in a semi-enclosed northern inlet. Estuarine, Coastal and Shelf Science 53: 107-121.

Piontkovski, S., Williams, R. and Melnik, T. (1995) Spatial heterogeneity, biomass and size structure of plankton of the Indian Ocean: some general trends. Marine Ecology Progress Series 117: 219-227.

Prins, T. and Smaal, A. (1994) The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde estuary, (The Netherlands). Hydrobiologia 282/283: 413-429.

Prins, T., Escaravage, V., Smaal, A. C., and Peeters, J. (1995) Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. Ophelia 41: 289-315.

Prins, T., Smaal, A., and Dame, R. (1998) A review of the feedbacks between bovalve grazing and ecosystem processes. Aquatic Ecology 31: 349-359.

Raby, D., Mingelbier, M., Dodson, J., Klein, B., Lagadeuc, Y., and Legendre, L. (1997) Food particle size and selection by bivalve larvae in a temperate environment. Marine Biology 127: 665-672.

Razouls, S., De Bovee, F et al. (1994) Are size spectra of mesozooplankton a good tag for characterizing pelagic ecosystems? Vie et Milieu 44(1): 59-68.

Riccardi, N. and Marriotto, L. (2000) Seasonal variation in copepod body length: a comparison between different species in the Lagoon of Venice. Aquatic Ecology 34: 243-252.

Riemann, B., Nielsen, T., Horsted, S., Bjornsen, P., and Steen, J. (1988) Regulation of phytoplankton biomass in estuarine enclosures. Marine Ecology Progress Series 48:205-215.

Rodhouse, P. and Roden, C. (1987) Carbon budget for a coastal inlet in relation to intensive cultivation of suspension feeding bivalve molluscs. Marine Ecology Progress Series 36: 225-236.

Rodhouse, P., Roden, C., Hensey, M., and Ryan, T. (1985) Production of mussels, *Mytilus edulis*, in suspended culture and estimates of carbon and nitrogen flow: Killary Harbour, Ireland. Journal of the Marine Biological Association of the U.K. 65: 55-68.

Roff, J., Turner, M. et al. (1995) Bactivory by tropical copepod nauplii: extent and possible significance. Aquatic Microbial Ecology 9: 165-175.

Roman, M. (1984) Utilization of detritus by the copepod *Acartia tonsa*. Limnology and Oceanography 29: 949-959.

Schneider, G. and Behrends, G. (1998) Top-down control in a neritic plankton system by *Aurelia aurita* medusae: a summary. Ophelia 48: 71-82.

Siokou-Frangou, I., Papathanassiou, E., Lepretre, A., and Frontier, S. (1998). Zooplankton assemblages and influence of environmental parameters on them in a Mediterranean coastal area. Journal of Plankton Research 20(5): 847-870.

Smaal, A., van Stralen, M., and Schulling, E. (2001) The interaction between shellfish culture and ecosystem processes. Canadian Journal of Fisheries and Aquatic Sciences 58: 991-1002.

Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, JM., and Bibent, B. (2001) Influence if shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon. Marine Ecology Progress Series 218:

Spencer, B., Kaiser, M., and Edwards, D. (1997) Ecological effects if intertidal Manila clam cultivation: observations at the end of the cultivation phase. Journal of Applied Ecology 34: 444-452.

Sprules, W. and Munawar. (1986) Plankton size spectra in relation to ecosystem productivity, size and perturbation. Canadian Journal of Fisheries and Aquatic Sciences 43: 1789-1794.

Stalder, L. and Marcus, N. (1997) Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. Marine Biology 127: 599-607.

Stenton-Dozey, J., Probyn, T., and Busby, A. (2001) Impact of mussel (*Mytilus galloprovincialis*) raft culture on benthic macrofauna, in situ oxygen uptake and nutrient fluxes in Saldanha Bay, South Africa. Canadian Journal of Fisheries and Aquatic Sciences 58: 1021-1031.

Suchman, C. and Sullivan, B. (2000) Effect of prey size on vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. Journal of Plankton Research 22(12): 2289-2306.

Sullivan, B. (1995) How does water column structure influence copepod populations in coastal marine systems? Bulletin of Marine Science 53(1): 240-246.

Tande, K., Drobysheva, S., Nesterova, V. et al (2001) Patterns in the variations of copepod spring abundance in the northeastern Norwegian Sea and Barents Sea in cold and warms years during the 1980s and 1990s. Ices Journal of Marine Science 57(6): 1581-1591.

Timko, P., de Young, B., and Foley, J. (1999). *Observations of currents, temperature and salinity in Charles Arm, Newfoundland* (Rep. No. 99-2). St. John's, NL: Department of Physics and Physical Oceanography, Memorial University of Newfoundland.

Todd, C. and Laverick, M. (1991). *Coastal marine zooplankton: a practical manual for students*. New York: Cambridge University Press.

Uye, S. (1994) Replacement of large copepods with small ones with eutrophication of embayments: causes and consequences. Hydrobiologia 292/293: 513-519.

Wiafe, G. and Frid, C. (1996) Short term temporal variation in coastal zooplankton communities: the relative importance of physical and biological mechanisms. Journal of Plankton Research 18(8): 1485-1501.

Vidal, J. (1980) Physioecology of zooplankton 1. Effects of phytoplankton concentration, temperature, and body size on the net production efficiency of *Calanus pacificus* and *Pseudocalanus* sp. Marine Biology 56(3): 111-134.

Zhou, M. and Huntley, M. (1997) Population dynamics theory of plankton based on biomass spectra. Marine Ecology Progress Series 159: 61-73.